Fear in the Domestic Fowl: Can Aversion be Measured?

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To my parents

Contents

Declaration

This thesis is my own composition, and the work presented in it entirely my own. All references and assistance from other individuals have been acknowledged.

Steven Mark Rutter, October 1989.

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Abstract

Aversion learning techniques developed by psychologists are being used increasingly by applied ethologists to measure aversion in domestic animals in an attempt to assess the suffering caused by modern husbandry practices. However, before these techniques are used to measure the aversiveness of commercial practices, it is important to determine their validity. The aim of the study reported in this thesis was to examine the validity of four aversion learning techniques for the assessment of the welfare of domestic fowl.

One strain of laying hens (T-line, a medium bodyweight hybrid) generally learnt to perform a *shuttle avoidance* response during a warning stimulus (WS) in order to avoid an impending looming stimulus (a rapidly inflating balloon). However, another strain (S-line, a light bodyweight hybrid) failed to learn the shuttle avoidance task. The technique cannot, therefore, be recommended for use in the assessment of the welfare of domestic fowl. The hens which failed to learn the shuttle avoidance task did show *conditioned suppression* of an operant response when the WS was presented (i.e. they suppressed responding even though the response was not punished), but a general suppression of operant responding made the results difficult to interpret. Consequently, conditioned suppression requires further research before its suitability for welfare assessment can be determined. Both strains of hens learnt a *one-way avoidance* task, but only after a considerable number of exposures to the aversive stimulus (exposure to the commercial practice of cage dusting). Given that this could result in habituation (which may confound the measurement of aversion), one-way avoidance cannot be recommended for welfare assessment. In contrast, a *passive avoidance* task (suppressing an operant response which would otherwise be punished during the presentation of a discriminative stimulus) was learnt by all of the birds tested after relatively few exposures to the aversive stimulus (cage dusting).

Of the four techniques investigated in this study, passive avoidance appears to be the most promising. Results from a few of the passive avoidance subjects

suggested that that technique was empirically valid (i.e. that it could differentiate between different levels of aversion). However, given that this conclusion was based on results from a small number of subjects, it is important to determine whether the technique can discriminate between different levels of aversion before it is used to as a measure of aversion in commercial conditions.

CHAPTER 1 The Assessment of Animal Welfare

1.1. Introduction

After the Second World War, new, intensive farming techniques were developed in the Western world in an attempt to increase the economic efficiency of animal production. Ruth Harrison's book, "Animal Machines: The New Factory Farming Industry", brought these 'factory farming' techniques to the attention of the public (Harrison, 1964). The outcry was so strong that the government was forced to act. It was clear that existing legislation was incapable of dealing with the complex ethical problems associated with intensive farming. As a result the government set up a committee under the Chairmanship of Professor F.W.R. Brambell to investigate the 'welfare' of intensively reared animals. The Brambell report (Command Paper 2836, 1965) recognized three states of suffering; discomfort, stress and pain, and stated:

> "Welfare is a wide term that embraces both the physical and mental well-being of the animal. Any attempt to evaluate welfare, therefore, must take into account the scientific evidence available concerning the feelings of animals that can be derived from their structure and functions and also from their behaviour." (Command Paper 2836, 1965).

However, there was little scientific evidence available to the committee, and consequently many of its recommendations were arbitrary. In the subsequent years, considerable effort has gone into the development and implementation of scientific techniques for assessing animal welfare, and a number of thorough reviews are available (Dawkins, 1980; Duncan, 1980; Duncan, 1981; Stephens, 1988). The following sections briefly describe the various approaches which have been adopted.

1.2. Health and production as indicators of welfare

Ill-health is an obvious sign that an animal may be suffering and that its welfare is reduced. For example, poor cage design can result in a high incidence of 'wear-and-tear' damage to both the feathers and the skin of laying hens (Tauson, 1978). However, the low incidence of intestinal parasites, avian tuberculosis and fowl typhoid in intensive egg production systems is partly due to the fact that birds in cages are separated from their droppings (Lindgren, 1978). Although such findings have clear implications for animal welfare, the simple fact that an animal is 'physically' healthy does not necessarily mean that it is not suffering. It is possible that an animal can be in perfect physical health, but show a number of behavioural symptoms which suggest that it may be suffering psychologically e.g. healthy zoo animals can show "bizarre" behaviour patterns, such as pacing backwards and forwards, bobbing up and down or masturbation (Dawkins, 1980).

Stress has been shown to have a catabolic effect on protein (Brown, 1967; Baxter and Forsham, 1972) and it could, therefore, be argued that the productivity of an animal (e.g. the eggs produced by a laying hen or the meat produced by a broiler) attests to it not being stressed (Draper and Lake, 1967). Productivity can be measured either in individual animals, or, as is more often the case, at the level of the whole farm. Clearly, the gross productivity of a farm is not a good indicator of welfare as some individuals may have a low productivity as a result of stress. Indeed, the economics of large scale production mean that animals are often kept in conditions in which their individual productivity is less than maximal, and increasing stocking density can increase the gross output per unit land, labour or capital, even though it may reduce the output per individual animal (Ewer, 1971). However, the fact that productivity can be measured in many different ways means that even individual productivity is not always a good indicator of animal welfare (Murphy, 1978a). Also, a animal may be highly productive (e.g. gaining weight with a relatively low food intake) either because it is kept in a restricted space and cannot move or because it is free from parasites or does not have to escape from frightening stimuli.

Therefore, although poor health and poor productivity can be used as indicators of poor welfare (Hughes, 1975a), good health and high productivity do not necessarily indicate good welfare.

1.3. Physiological indicators of welfare

The importance of the sympathetic nervous system in the mediation of physiological and behavioural responses to stress was first recognized by Cannon

(1929). He noted that when stressed the body prepared itself for physical exertion in what he termed the 'fight or flight' response (also known as the alarm reaction or general emergency reaction). Arousal of the sympathetic nervous system results in the release of catecholamines from the adrenal medulla. The catecholamines cause a number of secondary responses, including an increase in heart rate and the redistribution of blood in the tissues.

Prolonged stress leads to the general adaptation syndrome or GAS (Selye, 1950). This involves the secretion of adrenocorticotrophic hormone (ACTH) from the pituitary gland. ACTH stimulates the adrenal cortex to produce glucocorticoids, such as corticosterone. The glucocorticoids act on various tissues (such as the liver), and ensure that the body is provided with a readily available source of energy, namely blood glucose. In this respect, the GAS is, as its name suggests, adaptive, in that it prepares the animal for a possible confrontation with the source of the stress. However, if the stress is very prolonged, the adaptive mechanisms break down and the animal begins to suffer from the so-called diseases of adaptation such as stomach ulcers. It appears that the alarm reaction is relatively more important than the general adaptation syndrome in birds compared to mammals (Draper and Lake, 1967).

Ideally, research which used the alarm reaction as an indicator of stress (and therefore reduced welfare) would look at the primary responses i.e. increased activity in the sympathetic nervous system and adrenal medulla for the alarm reaction and increased secretion of ACTH for the GAS. However, these responses are very difficult to measure (Duncan and Filshie, 1979), and welfare studies have, therefore, looked at the secondary responses. For example, changes in heart rate have been recorded during catching in broilers (Duncan, Slee, Kettlewell, Berry and Carlisle, 1986). Baldwin and Stephens (1973) found that chasing a pig with an electric goad resulted in an increase in the levels of corticosteroids in the blood. Kilgour and de Langen (1970) found that social isolation in sheep resulted in a larger increase in plasma corticosteroids than that following a variety of husbandry procedures (e.g. being dipped or chased by a dog).

However, there are a number of problems associated with the use of physiological measures. The accurate measurement of often small physiological internal changes poses a considerable practical problem. Developments in micro-electronics and radio-telemetry have allowed some internal physiological parameters to be recorded with minimal disturbance to the test animal. For example, battery powered miniature radio transmitters have been sub-cutaneously implanted in domestic fowl, facilitating the accurate recording of heart-rate and

shank temperature (Filshie, Duncan and Clark, 1980). However, the instrumentation needed to measure endocrinological changes is still far too bulky to be implanted in any domestic animal. Measurement of the endocrine changes associated with stress still usually requires the animal to be caught and a blood sample taken. If this procedure is performed quickly, the stress caused by the sampling procedure itself may not effect the measurement of the stress resulting from the experimental treatment. However, the capture and restraint of test animals can seriously limit the potential of this technique, especially if more than one sample from each animal is required. Although the restriction imposed by certain intensive farming techniques (e.g. tethering sows) could actually facilitate the collection of blood samples with minimal disturbance to the animal (e.g. with the use of indwelling catheters), the results could not be compared with those from free-moving animals (which would have to be caught before a blood sample could be taken) as the action of catching the free-moving animals could stress them.

Although most of the practical problems associated with recording physiological changes will probably be overcome with future developments in micro-instrumentation, there are still theoretical objections against the use of physiological measures in the assessment of animal welfare (Rutter and Duncan, 1989). Although the state of fear is usually accompanied by, for example, an increase in heart rate, it does not follow that an increase in heart rate indicates that the animal is frightened. The state of excitement is often also accompanied by an increase in heart rate. Therefore, if one prohibits husbandry procedures which result in a minimal increase in heart rate, one will not only remove frightening stimulation but also any stimulation which the bird finds exciting (Rutter and Duncan, 1989). This could be detrimental to the birds' welfare as it may lead to the state of boredom, which may itself be aversive (Wemelsfelder, in press).

1.4. Behavioural indicators of welfare

There are two ways in which the behaviour of an animal can be used to assess its welfare.

1.4.1. Inappropriate behaviour

The first method involves comparing the behaviour of animals under "ideal" conditions with that found under commercial conditions, and then independently showing that any differences in behaviour are indicative of reduced welfare (Hughes, 1976). For example, dust-bathing, ground-scratching, wing-flapping and body and tail shaking occur less in cages than in deep-litter pens (Wennrich and

Strauss, 1977), but caged birds perform more preening and wing or leg stretching than those kept in deep-litter pens (Hughes and Black, 1974). Vestergaard (1978) found that although wire floors reduced fighting, they increase aggressive pecking. Battery caged hens also show more head-flicking than those kept in a deep-litter system (Bareham, 1972).

There are a number of problems with this approach. The first problem arises in trying to decide what constitutes an 'ideal' environment. Given that domestication has resulted in changes in the behaviour of domestic animals compared to their wild counterparts (Kretchmer and Fox, 1975), the "wild" or "natural" environment is not necessarily the "ideal" environment (Duncan, 1981). This problem could, to some extent, be overcome by investigating the behaviour of the wild progenitor of domestic species in a domestic environment (e.g. Desforges and Wood-Gush, 1975) and the behaviour of domestic animals in wild or "natural" habitats (e.g. Duncan, Savory and Wood-Gush, 1978). Secondly, it is difficult to show that any differences in behaviour are indicative of reduced welfare. For example, Hughes (1983) found that head-shaking in domestic hens was increased when they were exposed to novel or disturbing stimuli and concluded that head-shaking is an "alerting response" and is not necessarily indicative of reduced welfare. Finally, the results from this method of investigating animal welfare can be difficult to interpret. For example, the simple fact that a behaviour pattern is missing in animals kept in a particular environment does not necessarily imply that that environment "prevents" the behaviour pattern from occurring. It is possible that the environment does not "release" the behaviour or that the animal simply does not "want" to perform the behaviour in that particular environment (Duncan, 1980).

1.4.2. Experimental exposure to stressful situations

An alternative behavioural approach involves subjecting animals to stressful situations under controlled conditions in the laboratory, and comparing this behaviour with that found under commercial conditions. If the animals show fear or frustration reactions when exposed to a certain situation, that situation can be assumed to be frightening or frustrating. For example, when domestic fowl are severely frustrated experimentally, they show stereotyped back-and-forward pacing (Duncan and Wood-Gush, 1972a) and increased aggression (Duncan and Wood-Gush, 1971). When the frustration is mild, they show increased displacement preening (Duncan and Wood-Gush, 1972a). In battery cages, some birds show symptoms of severe frustration in the pre-laying period, suggesting

that their may well be welfare problems at this particular time. All birds show symptoms of mild frustration at various times, and it could be argued that this indicates their welfare is generally threatened by caging. However, hens also show these symptoms in "natural" environments, and it is possible that they may simply be the "bird's way of responding to everyday problems" (Duncan, 1981). Although this approach can indicate that problems exist in a given situation, they do not necessarily indicate if the animal is suffering.

The reactions of hens to frightening stimuli are varied (Murphy, 1978b; Duncan, 1985) and can include escape attempts, freezing and vocalization. The fact that fear reactions are so varied means that they can be difficult to quantify and interpret e.g. an animal may freeze when exposed to one stimulus, but run away from another. However, it may be possible to gauge the level of fear in domestic fowl by measuring the duration of artificially induced immobility, usually known as 'Tonic Immobility' or TI. TI has been studied extensively by Gallup (see Gallup, 1977 for a review), and has been shown to be positively correlated with other measures of fear in domestic hens (Jones, 1986; Jones, 1987a). However, the induction of TI requires the experimenter to capture and physically restrain the animal and such interference can seriously confound the measurement of the fear resulting from the experimental treatment (Murphy, 1978b).

1.5. The animal's 'feelings' and its welfare

Although the psychological aspects of animal welfare have been emphasized for a number of years (Dawkins, 1980; Baxter, 1983; Zayan and Duncan, 1987), Duncan and Petherick (1989) have recently argued that welfare is *purely* a question of how the animal 'feels' i.e. it is solely concerned with psychology. They gave the example of a person with tooth decay. In this situation, the person's welfare only becomes diminished when they discover that something is wrong, either by the tooth becoming painful or by being told of the problem by a dentist. Until that point is reached, the person's welfare (at least with regard to his/her teeth) is all right. Similarly, as long as farm animals 'feel' all right, then their welfare is all right. As long as the animal's "cognitive needs" are met, its physical needs do not matter. In many respects, this idea is just a matter of common sense, and one with which I agree. However, Duncan and Petherick's (1989) viewpoint is still not accepted by a number of applied ethologists (D.M.Broom, pers.comm.; L.Braithwaite, pers. comm.), and their approach faces a number of difficulties which are discussed later.

1.5.1. Fear vs aversion

The fact that, in a given situation, an animal shows both physiological and behavioural signs of fear does not necessarily mean that it finds that situation aversive or unpleasant (Rutter and Duncan, 1989). For example, human beings actually seem to enjoy some 'frightening' situations, for example watching horror movies or going on fairground rides. Under these circumstances, people show both physiological and behavioural responses usually associated with the state of fear e.g. increased heart rate and screaming. Although such responses may be due to excitement, people usually say that they find such experiences frightening. However, the simple fact that they are prepared to endure such stimulation again and again suggests that they do not find it aversive. It could be argued that the derivation of pleasure from fear is peculiar to humans. However, Humphrey (1972) found that rhesus monkeys would continue to press a lever to be shown photographs and moving pictures even though these pictures caused them to show overt signs of fear i.e. "their ears lay back, their hair stood on end, they urinated, and their posture and faces expressed great anxiety". Again, the fact that they continued to work to be given such stimulation suggests that they did not find it aversive.

Indeed, many of the problems associated with the concept of fear (e.g. Murphy, 1978b; Jones, 1987b) can be overcome by using the concept of aversion. Fear has been described, amongst other things, as a hypothetical intervening variable (Broadhurst, 1960), a hypothetical state of the brain or neuroendocrine system (Gray, 1971), a motivating, acquirable drive (Miller, 1948), or an adaptive psychophysiological response to perceived danger (Jones, 1987b). In contrast, aversion is simply a "mental attitude of opposition or repugnance" (OED), that is a 'dislike'. It is important to emphasize that term aversion is *not* simply a replacement for the term fear (cf. Murphy, 1978b). Aversion is a different, far simpler concept which, as a purely *psychological* phenomenon, is more suited to Duncan and Petherick's (1989) concept of welfare (discussed earlier) than is the concept of fear. Whilst animals can find frightening situations aversive (although, as discussed earlier, this need not always be the case), they can also find other situations (e.g. frustration or boredom) aversive.

1.5.2. Determining how animals 'feel'

The main problem with a 'cognitive' approach to the assessment of animal welfare is that mental experiences are private and are not open to inspection from outside. Indeed, it is impossible to know if fellow human beings experience the

same 'feelings' as oneself. One can only assume that, because other people behave in a similar way to oneself, that they also experience similar feelings. Similarly, it is impossible to determine whether animals experience mental states. Consequently, mental states such as aversion and pleasure cannot, strictly speaking, be measured, and this problem will be discussed further in Chapters 3 and 9. However, Humphrey's (1972) experiment demonstrates a promising approach which, to some extent, can be used to assess the subjective feelings of animals. This is to see if particular treatments will act as reinforcement[1], either positive (e.g. a food reward) or negative (e.g. a punishing electric shock), for the learning and maintenance of new behaviour patterns (Dawkins, 1980). Such an approach benefits from the fact that it does not require any prior assumptions to be made about the properties (either positive or negative) of the treatment under investigation as these properties can be determined empirically.

1.5.3. Preference tests

The simplest way to determine what an animal finds rewarding is to give the animal a choice in a preference test. For example, Dawkins (1976, 1977) found that when hens were given a choice between a commercial battery cage or an outside run, the hens preferred the run, although the choice was strongly influenced by prior experience i.e. the birds initially chose what was familiar. Similarly, hens prefer larger rather than smaller cages (Hughes, 1975b; Dawkins, 1978), a cage with a grass floor to one with a wire floor (Dawkins, 1978), an empty cage or one containing a small number of strange (i.e. unfamiliar) hens to one containing a large number of strange hens (Hughes, 1977), and a cage containing familiar hens rather than one containing strange hens (Hughes, 1977). Hughes and Black (1973) showed that given a choice of four floor types, the order of preference shown by hens was (i) an hexagonal wire netting floor, which was condemned by the Brambell Committee (Command Paper 2836, 1965), (ii) a conventional mesh floor made with heavy gauge steel, which was recommended by the Brambell Committee (Command Paper 2836, 1965), (iii) a conventional mesh floor, and, (iv) a perforated sheet steel floor. This demonstrates the danger of making recommendations on animal welfare which are not based on scientific evidence.

Choice tests can also be used to determine the aversiveness of husbandry procedures. For example, Rushen (1986a) used a paired-choice test to determine

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[1] Dawkins' (1980) use of the terms positive and negative reinforcement differ from the traditional psychological definition of the two terms, which is discussed in Chapter 2. However, this thesis will follow Dawkins (1980) usage.

the preference of sheep for different handling procedures. The rank order of treatments (in decreasing preference) was: human contact, physical restraint in the presence of other sheep, isolation, capture in isolation, and inversion in isolation.

Another technique which can be used to assess the preferences of an animal is operant conditioning. This involves training the animal to perform a certain response (e.g. a hen pecking a plastic disc or a pig pushing a panel) in order to gain access to a reward. Operant conditioning has been used with domestic fowl to assess the preferred cage size (Faure, 1986), the preferred type of cage floor (Faure, 1986; Lagadic and Faure, 1987), the preferred lighting level (Savory and Duncan, 1982) and the preferred thermal environment (Morrison and McMillan, 1985).

Duncan (1978) has criticized preference tests on three grounds. Firstly, preference tests provide only a relative measure; the fact that A is chosen in preference to B tells us nothing about the absolute properties of A and B, or how important any preference is to the animal. This problem was summarized by Dawkins (1980) when she pointed out that "a gourmet might prefer caviare to smoked salmon, but it would be difficult to argue that he would suffer if he had to make do with smoked salmon". Secondly, the choice an animal makes may only reflect its short-term requirements, and animals "cannot be expected" to make choices based on their long-term consequences (Duncan, 1978). For example, hens will enter trap-nests in order to lay, even though this results in them being confined without food and water for several hours after oviposition (Duncan, 1978). Finally, the results from preference tests can be difficult to interpret. The fact that an animal chooses A in preference to B on 90% of the trials does not mean that choosing B on the remaining 10% of trials is not important to the animal.

1.5.4. Consumer demand theory

These criticisms led Dawkins (1983) to propose a slightly different approach to assessing animal welfare. This was to see what 'price' animals are prepared to pay, either to gain access to a positive reinforcer or to avoid a negative reinforcer. This allows animals to show, through their behaviour, how important it is to gain access to or to avoid certain situations (Dawkins, 1988). If the animal's preference is still apparent when it has to pay a higher price, then the animal is said to show "inelastic demand" (Lea, 1978; Hursh, 1984), "compensation" (Hogan and Roper, 1978) or "resilience" (McFarland and Houston, 1981). Such inelastic demand suggests that the 'commodity' in question is very important to the animal.

One way of determining the price an animal is prepared to pay in order to gain access to something is again to use operant conditioning, but to show that an animal is prepared to work harder for the same amount of reward i.e. determine if it has an inelastic demand. For example, animals will work harder for the same size of food reward (Hogan, Kleist and Hutchings, 1970; Marwine and Collier, 1979; Hursh, 1984), but will not work harder to gain access to a rival (Hogan *et al*, 1978) or for gaining light (Findley, 1959). Animals will generally work harder for the same amount of water as a reward (Hogan and Roper, 1978), although some animals which are adapted to dry environments will not (Boice, 1984).

There are a number of problems with this approach. Firstly, animals have some difficulty in learning the association between certain responses and certain rewards. For example, Dawkins and Beardsley (1986) found that hens could not learn to peck at a key in order to gain access to litter, although they could learn (after extensive training) to break a photobeam in order to gain access to litter. Such constraints on learning have serious implications for the practical application of these techniques, and these are discussed in Chapter 3. Also, one of the problems raised by Duncan (1978) still remains i.e. a short-term choice may not reflect the animal's long-term preference. However, this problem can be overcome by studying animals' demands over a longer period of time, giving them the opportunity to continuously adjust their behaviour (Collier, Hirsch and Hamlin, 1972). This involves studying and manipulating the animals' 'time budgets' i.e. the amount of time the animal devotes to various activities, and this is a promising approach to assessing the effects of deprivation (i.e. suffering as a result of the absence of stimuli which the animal 'needs') on animal welfare (Dawkins, 1988).

1.5.5. Aversion learning

Just as operant conditioning can, to some extent, be used to determine what an animal finds rewarding, the technique can also be used to find out what an animal finds aversive or punishing. For example, Rushen (1986b) punished sheep for running down a race with either electroimmobilization or physical restraint. After four treatments, the sheep which had received electroimmobilization took longer to "push-up" to the start of the race and longer to run down the race than those which had received physical restraint. Consequently, Rushen (1986b) argued that the sheep found electroimmobilization more aversive than physical restraint. It is possible to measure how aversive an animal finds a particular treatment by "titrating" positive against negative reinforcement. For example, Dill (1987) demonstrated that fishes make adaptive "trade-offs" between food

availability and the risk of predation in their selection of feeding sites. Such techniques appear to be a promising approach to the assessment of aversion (Dawkins, 1988).

1.6. Summary

Dawkins (1988) divides suffering into two categories: deprivation and aversion. The analysis of time budgets appears to be the most promising approach to assessing the effects of deprivation, and aversion learning appears to be the most promising approach to assessing the effects of aversion (Dawkins, 1988). However, before using aversion learning techniques to assess animal welfare under commercial conditions, it is important to determine their validity as measures of aversion (Rushen, 1986c). This thesis aims to do just this.

Kerlinger (1973) discusses various techniques for assessing the validity of a psychological test. The absolute test of a psychological measure is its 'construct' validity i.e. to establish a theoretical link between the behavioural response and the subjective experience, and, with this aim in mind, the following chapter reviews aversion learning theory.

CHAPTER 2 Aversion Learning: Theory

2.1 Introduction

The ultimate test of any psychological measure is to assess its 'construct' validity, that is to establish a theoretical link between the behavioural response and the subjective experience (Kerlinger, 1973). With this in mind, this chapter briefly reviews aversion learning theory.

2.2. Pavlovian vs instrumental conditioning

Animal learning theory can be divided into two principal areas: Pavlovian (also known as classical, respondent or Type I) conditioning and Instrumental (also known as operant or Type II) conditioning.

2.2.1. Pavlovian conditioning

Most people immediately associate the term conditioning with the work of the Russian physiologist, Ivan Pavlov (1927). He studied the salivary reflex of the dog, collecting saliva directly from the salivary gland through a fistula in the animal's cheek. The dogs would salivate when small amounts of powdered meat were introduced into their mouths. Immediately prior to the delivery of the food, Pavlov exposed the animal to some stimulus e.g. the ticking of a metronome. On the first exposure to the novel stimulus the dogs showed little reaction, other than perhaps pricking up their ears. Once the meat powder was introduced into the animal's mouth saliva would be produced. However, after the procedure had been repeated a few times, the dogs started to salivate when the metronome started ticking and before food entered their mouths. The dogs had learnt that the metronome preceded food and could, therefore, anticipate its delivery.

As salivation during the metronome was conditional on the animal learning the association between metronome and food, Pavlov termed this the 'conditional

response' (later abbreviated to CR). Salivation in response to food delivery itself did not depend on the animal learning this association, and was, therefore, termed the unconditional response. The stimulus which elicited the conditional response (e.g. the metronome) was termed the conditional stimulus; and the stimulus which caused the unconditional response (e.g. food) was called the unconditional stimulus. Unfortunately, when Pavlov's work was first translated from Russian into English, the word conditional was incorrectly translated into conditioned. Hence, the conditional stimulus became the conditioned stimulus, or CS for short; and the unconditional stimulus the unconditioned stimulus or US. Shortly after, scientists in the West started to refer to Pavlov's work as Pavlovian conditioning. Although the origin of the term conditioning was therefore accidental, it was soon in common use[1].

2.2.2. Instrumental conditioning

Whilst Pavlov was working on his reflex 'conditioning', an American researcher, Edward Thorndike (1911), was studying learning in cats. He used a variety of 'problem boxes', each with a spring-loaded door. Each door was held shut by a latch, and could only be opened if the subject performed a given response, for example, pressing a lever. When a cat was shut in the box, it would attempt to escape, moving about restlessly. Eventually, it would step on the lever and the door would swing open, allowing it to escape. After a number of such trials, the cat eventually learnt, through trial and error, that lever pressing was the only behaviour which opened the door. When next placed in the box, the cat moved swiftly across the box, pressed the lever and escaped. As the cat was instrumental in causing the event which allowed then to escape, namely opening the door, Thorndike's work came to be known as Instrumental conditioning.

The principal difference between Pavlovian and Instrumental conditioning is in the role of the subject in the conditioning procedure. Under a Pavlovian paradigm, the subject has no control over the presentation of the external stimuli. Under an Instrumental paradigm, the subject can control the occurrence of events by performing certain patterns of behaviour. This distinction has been prominent in

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[1] It has recently become fashionable to return to using Pavlov's original terminology (McFarland, 1985). However, this can lead to some confusion, and it is difficult to know where to draw the line e.g. does conditioned suppression become conditional suppression? Given that the majority of the psychological literature uses the abbreviations CS and US (often without definition), I shall follow their lead. The reader can, therefore, read CS as either the conditional or conditioned stimulus, whichever pleases.

the development of learning theory. However, in recent years, theorists have questioned its importance. For example Dickinson (1980) prefers to consider that animals learn general associations of the form E1 → E2. E1 can be the CS and E2 the US under a Pavlovian paradigm, or E1 can be some response the subject performs to receive an instrumental reinforcer, E2.

2.2.3. Pavlovian vs instrumental reinforcement

The term reinforcement was originally used by Pavlov (1927). He used the term to refer to events which acted to strengthen a response. For example, food, a positive reinforcer, acts to increase the secretion of saliva in the mouth. The delivery of an electric shock to a dog's paw, a negative reinforcer, acts to increase the reflexive withdrawal of the paw. Consequently, the difference between positive and negative reinforcement was based on the intrinsic characteristics of the stimulus. For example, the delivery of acid to the animal's mouth also acts to increase saliva secretion. However, Pavlov considered the delivery of acid to be a negative reinforcer as it involved a different mechanism of salivary secretion (i.e. defensive as opposed to appetitive).

Such a definition of reinforcement is, however, inadequate in considering instrumental conditioning, where the occurrence of certain events can result in a decrease in the frequency of a response. Thorndike (1911) used the terms "satisfiers" and "annoyers" to describe stimuli which acted to increase or decrease the probability of the occurrence of a response respectively. Consequently, the difference between 'satisfiers' and 'annoyers' was determined by their effects on behaviour and not by any intrinsic properties of the stimuli themselves. However, the term reinforcement was subsequently used in accounts of instrumental conditioning (e.g. Ferster and Skinner, 1957). Although the term positive reinforcement was applicable to both classical and instrumental conditioning (i.e. in both cases it acted to increase the frequency of a response), the classical definition of negative reinforcement was not applicable to instrumental conditioning.

Mackintosh (1983) defines a reinforcer as "an event whose occurrence in relation to other events supports some change in behaviour". An appetitive reinforcer (e.g. food) acts to increase the probability of an response occurring, whereas an aversive reinforcer (e.g. electric shock) acts to decrease the probability of the response occurring. This definition is, therefore, similar to Thorndike's (1911) distinction between satisfiers and annoyers in that it is purely behavioural. However, Mackintosh (1983) uses this definition for both

instrumental and classical reinforcement, even though this does "some violence to the etymology" (Mackintosh, 1983).

In this thesis, I will use Mackintosh's (1983) definition of reinforcement, although I will follow Dawkins' (1980) lead in using positive and negative reinforcement instead of Mackintosh's appetitive and aversive reinforcement.

2.3. Avoidance theory

Although appetitive conditioning has been more widely studied than aversive conditioning, theoretical considerations of avoidance learning have taxed learning theorists since the 1920s.

2.3.1. Pavlovian accounts of avoidance

The ability of an animal to avoid an aversive stimulus was first demonstrated, albeit fortuitously, by Bekhterev in 1913 (Razran, 1956). Working at the same time as Pavlov, Bekhterev studied what later became known as motor conditioning. A dog would first be exposed to some neutral stimulus, which was then followed by a delivery of an electric shock to the animal's paw, causing the dog to withdraw its leg. After this procedure had been repeated a few times, the dog would withdraw its paw as soon as the neutral stimulus came on and before the shock was actually delivered. What Bekhterev did not realize was the importance of whether or not the withdrawal of the paw terminated the shock, i.e. whether or not the animal could actually *avoid* the shock. From the account given by Razran (1956), it appears that the withdrawal response sometimes was and sometimes was not an effective avoidance response.

Hull's (1929) account of such motor conditioning also failed to take this distinction into account; it was purely in terms of Pavlovian conditioning, the withdrawal of the leg was seen as a CR to the CS. The avoidance response could be simply considered to be a reduced latency escape response. Subsequent studies have, however, shown that animals can learn an avoidance response which is different to the response required to escape from the aversive stimulus. Mowrer and Lamoreaux (1946) showed that rats could learn to run in order to avoid an electric shock, even though jumping was the only effective escape response once the shock had started. Bolles (1969) demonstrated this result holds true for a variety of different responses.

2.3.2. Instrumental avoidance theory

It was Schlosberg (1934) who first realized the importance of whether or not the response terminated the shock. He compared two procedures using the tail-flick response in rats, one where the subject could avoid shock by tail-flicking, the other where it could not. Unfortunately, he found little difference in the extent of the conditioning under the two conditions. However, a year later Hunter (1935) was able to demonstrate that such behaviour was more readily conditioned if the response did terminate the electric shock. Brogden, Lipman and Culler (1938) studied the two conditions (Figure 2.1) using the wheel running response in the guinea pig. Subjects which could avoid the shock responded consistently, eventually reaching 100% performance. Whilst the other group initially showed similar performance, they soon fell behind and even started to show a reduction in responding towards the end of the experiment.

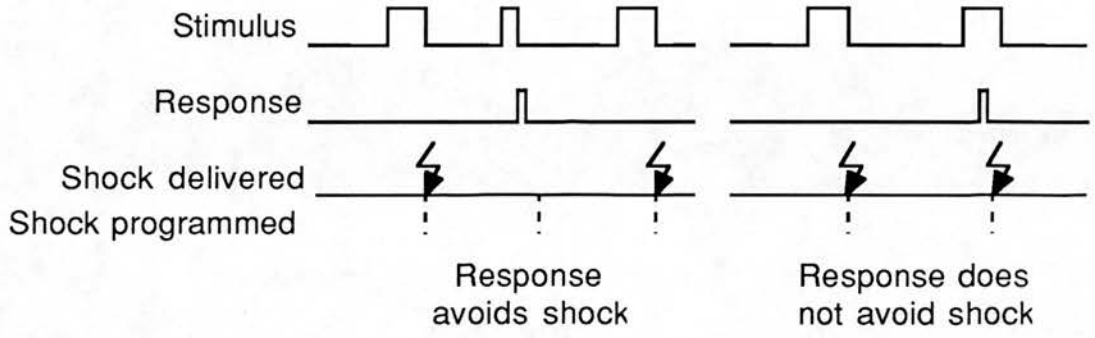

Figure 2.1. Diagrams of the two procedures used by Brogden, Lipman and Culler (1938). (From Herrnstein, 1969).

These findings lead Mowrer (1939) to the conclusion that avoidance was really an example of Thorndike's Law of Effect. In his words:

> "The position here taken is that human beings (and also other living organ[ism]s to varying degrees) can be motivated either by organic pressures (needs) that are currently present and felt *or* by the mere anticipation of such pressures and that those habits tend to be acquired and perpetuated (reinforced) which effect a reduction in *either* of these two types of motivation. This view rests upon and is but an extended application of the well-founded law of effect and involves no assumptions that are not empirically verifiable."

The subject, therefore, performed the avoidance response because it learnt, through instrumental conditioning, that the performance of the response prevented the occurrence of the aversive event, i.e. that by performing the response the subject was instrumental in preventing the delivery of an electric shock.

However, this purely instrumental theory of avoidance soon encountered a major problem. Once an animal had learnt the avoidance response it effectively placed itself on an extinction schedule, i.e. the animal no longer received the electric shocks which were supposedly reinforcing avoidance. This problem was summarized by Schoenfeld (1950) when he asked "how the non-occurrence of an unconditioned stimulus can act as reinforcement ?" Even Mowrer (1947) himself had realized the problem :

> "It had previously been taken for granted by various writers that it is in some manner rewarding to an experimental subject to avoid a noxious unconditioned stimulus. It is easily seen that it is rewarding to escape from such a noxious stimulus. But how can a shock which is *not experienced*, i.e. which is avoided, be said to provide either a source of motivation or of satisfaction?" (Mowrer, 1947)

2.3.3. Two-factor theory

The lack of tangible reinforcement for his instrumental avoidance theory resulted in Mowrer revising it and proposing the first two-factor theory of avoidance. It was based on both instrumental and Pavlovian conditioning (Mowrer, 1947, 1960). He suggested that a subject first learns an association between the CS and the US such that the CS comes to elicit fear. This is the classically conditioned stage. The subject then learns that the performance of the avoidance response results in the termination of the CS. This is the instrumental stage, with the reduction in fear, as a result of CS termination, providing the positive reinforcement necessary for instrumental learning.

However, in 1953, Sidman demonstrated that rats could learn to avoid electric shock without any exterioceptive warning signal. He taught rats to depress a lever in order to avoid an electric shock. However, the rats were not given any exterioceptive warning that, unless they responded soon, a shock would be delivered. Each shock was programmed to occur 20 seconds after the previous shock, unless the animal performed a response, which postponed the shock for 20 seconds. The rats could, therefore, avoid shocks by performing the response at least once every 20 seconds. Although the fact that avoidance learning was possible without an explicit CS, Sidman (1953) still referred to the two-factor theory in his account of this experiment. He believed that any behaviour the rat performed, other than lever pressing, was paired with shock and that this 'non-avoidance' behaviour, therefore, acted as a CS. The performance of the avoidance response resulted in the termination of this 'non-avoidance' behaviour which provided the reinforcement for the instrumental stage.

Anger (1963) proposed a different account of unsignalled avoidance. He suggested that an internal temporal stimulus (the time since the last response) built up in the interval between responses. This became increasingly aversive as the time interval lengthened. Performance of an avoidance response acted to 'reset' this internal 'clock', with the corresponding reduction in fear instrumentally reinforcing the response.

2.3.4. Expectancy theory

Hilgard and Marquis (1940) proposed a simple and common-sense theory of avoidance, i.e. that an avoidance response is reinforced because it avoids an aversive event. In their words:

> "Learning in this [avoidance] situation appears to be based in a real sense on the avoidance of shock. It differs clearly from other types of instrumental training in which the conditioned response is followed by a definite stimulus - food or the cessation of shock. In instrumental avoidance training the new response is strengthened in the absence of any such stimulus; indeed, it is strengthened because of the absence of such a stimulus. Absence of stimulation can obviously have an influence on behaviour only if there exists some preparation for or the expectation of the stimulation."

This is an appealing account of avoidance behaviour. The idea that animals form expectations was first proposed by Tolman (1932). However, such a cognitive interpretation of animal behaviour was shunned by the behaviourists. In Guthrie's (1935) words "the rat is left buried in thought". More recently, learning theorists are returning to Tolman's views on learning (Gray, 1975; Bolles, 1989), and this may prove to be the most promising approach to the avoidance learning problem.

2.3.5. Species-specific defence reaction theory

It became apparent in the 1960s that animals learnt certain avoidance tasks more readily than others. For example, pigeons can only be taught to peck a key to avoid shock after extensive and elaborate shaping (e.g. Hineline & Rachlin, 1969). However, rats can learn to jump out of a box in order to avoid an electric shock in just one trial (e.g. Maatsch, 1959). Such findings led Bolles (1970, 1971) to propose that the poor performance encountered with certain aversion learning tasks was due to what he termed 'species-specific defence reactions', or SSDRs. He believed that each species had a repertoire of innate, natural defence reactions and proposed that the animal would find it difficult to learn an avoidance task if it was not one of these innate reactions. For example, he proposed that key-peck avoidance in pigeons is not readily learnt because key-pecking is not a natural

defence reaction. If a pigeon does eventually learn a key-peck avoidance task, the pecks are directed towards the key in an aggressive manner i.e. the response shows characteristics of an SSDR. If, however, the response was a natural defensive reaction for the subject, for example a one-way locomotor response, then the animal would be expected to learn the task. Crawford and Masterson (1978), however, demonstrated that rats which were allowed to move (or were moved by the experimenter) to a safe location within seven seconds of bar-pressing showed unusually high rates of bar pressing in order to avoid an electric shock. Given that the enhanced source of reinforcement (i.e. being moved to a safe place) nullified the effects of the impending SSDR, Crawford and Masterson (1978) concluded that their results contradicted Bolles' (1971) SSDR hypothesis.

2.3.6. Defence motivation theory

The deficiencies that Crawford and Masterson (1978) found in Bolles' (1971) SSDR hypothesis lead them to propose their own theory of avoidance behaviour (Masterson and Crawford, 1982). This was based on a consummatory stimulus reward hypothesis, which assumes that aversive stimulation acts to increase the probability of defence reactions occurring (i.e. it is similar to Bolles' [1971] SSDR hypothesis) and also to activate representations of relevant consummatory stimuli[1]. Positive reinforcement is provided when the there is a match between the stimuli the subject encounters and the internal representation of consummatory stimuli. Just as food deprivation induces food-seeking behaviour and makes food-related stimuli positively rewarding, aversive stimulation induces defensive responses which make stimuli related to flight positively reinforcing. Therefore, animals can learn non-SSDR avoidance tasks given the positive reinforcement derived from flight related stimuli.

However, as Modaresi (1989) points out, Crawford and Masterson (1978) used a number of techniques which were designed to reduce freezing and bar holding and to promote frontal bar pressing prior to testing. These included the use of a modest shock intensity (Bolles and Warren, 1965), punishing bar holding (Feldman and Bremner, 1963), use of a retractable lever (Cole and Fantino, 1966), and appetitive bar press training prior to testing (Giulian and Schmaltz, 1973), which act to change the rat's defence response repertoire (Anisman and Waller,

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[1] A consummatory stimulus is a stimulus which will support innate consummatory responses. For example, rats will learn to press a lever to open a door through which they can run in order to avoid an electric shock (Masterson, 1970) i.e. they will respond to obtain consummatory escape route stimuli that support innate flight reactions (Masterson and Crawford, 1982).

1973). Modaresi (1989) showed that without these additional techniques, rats which could move to a safe place only showed improved bar-press avoidance at very low shock intensities. This suggests that the role of SSDRs in avoidance learning is more important then Masterson and Crawford (1982) suggest.

2.4. Punishment theory

In comparison to avoidance theory, punishment theory has received little attention.

2.4.1. The negative 'Law of Effect'

The first theory of punishment was Thorndike's (1913) Negative Law of Effect. The empirical law stated that just as responses which were followed by 'satisfiers' increased in probability (the positive Law of Effect), responses followed by 'annoyers' decreased in probability. The theoretical negative Law of Effect stated that the decrease in the probability of the responses which were followed by 'annoyers' was due to the weakening or loss of bonds or connections i.e. the response was essentially 'unlearnt'.

However, both the theoretical and empirical versions of the negative Law of Effect were later abandoned by Thorndike (1931, 1932) because he found, amongst other things, that a 30 second confinement following incorrect choice did not stop an animal making that choice again (Thorndike, 1932). This suggested to Thorndike that punishment simply did not work. However, later studies using more severe punishment (e.g. Estes, 1944) demonstrated that the empirical law was valid i.e. response contingent aversive stimulation did reduce the probability of the response occurring. Although recent studies have shown that not all responses are suppressed by punishment (e.g. Walters and Glazer, 1971), the empirical negative Law of Effect generally remains true (Mackintosh, 1974).

2.4.2. Classical punishment theory

One of the main objections against Thorndike's theoretical negative Law of Effect was that it involved the weakening of stimulus-response (S-R) connections through 'unlearning'. However, S-R theory only allows for the strengthening of S-R bonds through learning. Guthrie (1935) proposed that the suppression of the punished response was a result of the formation of new S-R bonds and the new response competed with and eventually suppressed the punished response. In Guthrie's (1935) own words:

"Sitting on tacks does not discourage learning. It encourages one in learning to do something else than sit. It is not the feeling caused by punishment, but the specific action caused by punishment that determines what will be learned."

The aversive stimulus can be seen as a US which elicits a number of defensive responses e.g. flinching or even running. Stimuli which are associated with the punished response will therefore act as CSs, eliciting a CR which will compete with the punished response and result in its suppression. However, the fact that response contingent shock results in greater response suppression than non-contingent shock (e.g. Church, 1963) suggests that instrumental learning is involved, to some extent, in the process of punishment.

2.4.3. Escape hypothesis theory

Dollard and Miller (1950) proposed that any new responses that occur after the onset of the aversive stimulus might be superstitiously associated, through instrumental conditioning, with the termination of the aversive stimulus. This was known as the 'escape hypothesis' theory. However, very brief electric shock can act as an effective punishing stimulus (e.g. Wischner, Fowler and Kushnick, 1963). Consequently, it is very unlikely that any discrete response would occur during brief exposure to the aversive stimulus, and the escape hypothesis theory can, therefore, be discounted.

2.4.4. Two-factor punishment theory

Two-factor punishment theory was based on Mowrer's (1947, 1960) two-factor avoidance theory (discussed earlier). Mowrer (1960) proposed that a state of fear is classically conditioned to stimuli which precede the punished response. If the subject performs a response which is incompatible with the punished response, the antecedent stimuli will change from those associated with a high probability of shock to those associated with a low probability of shock, and such stimuli will therefore elicit less fear. Consequently, the decrease in fear as a result of the performance of the incompatible response will instrumentally reinforce such a response, the performance of which will increase in probability, thus competing with and suppressing the punished response. However, as Mackintosh (1974) points out, this is an "extraordinarily complicated chain of events to account for what is ... a rather simple phenomenon", and can probably be dismissed

2.4.5. Negative incentive theory

Estes (1969) proposed a theory of punishment which was based on the symmetry between appetitive and aversive reinforcement. Just as the formation of an association between an instrumental response and an appetitive reinforcer may lead to an increase in the performance of the instrumental response, so the formation of an association between an instrumental response and an aversive reinforcer may lead to a suppression of the instrumental response as a result of an increase in the proximity of aversive reinforcement. This theory is supported by a number of studies which demonstrate the similarity in the associative processes underlying the effects of reward and punishment. For example, schedules of reinforcement that produce one pattern with appetitive reinforcement produce a complementary pattern with aversive reinforcement (Ferster and Skinner, 1957; Appel, 1968). Extinction reverses the effects of prior conditioning i.e. the omission of positive reinforcement results in a decrease in the performance of the response, whereas omission of a negative reinforcer results in recovery of the punished response (Estes, 1944). Consequently, this may prove the most promising theoretical approach to punishment.

2.5. Summary

Although aversion learning theory has come a long way in the last seventy years, it is still very much in its infancy, and many questions still remain unanswered. It is important to emphasize that I do not intend to address these questions in this thesis (although Bolles' [1971] SSDR theory will be discussed further in Chapter 5). The principal aim of this chapter was to show that contemporary animal learning theory is not sufficient to establish the construct validity of aversion learning techniques i.e. we cannot yet establish a theoretical link between the behavioural response and the motivation behind it. However, the discussion of the results from the various experiments reported in this thesis will reflect the contemporary view of animal learning i.e. that learning is a cognitive process (Bolles, 1989).

CHAPTER 3 Aversion Learning: Practice

3.1. Aversion learning techniques and terminology

There has been some confusion in a number of recent papers, written by applied ethologists, which describe aversion learning techniques. Such confusion principally arises over the distinction between classical and operant aversive conditioning techniques. For example, in a section entitled "Aversive classical conditioning", Rushen (1986c) talks about the "conditioned acceleration" procedure which "involves training the animal to perform some behaviour ... not to obtain a food reward but to *avoid* another electric shock" (Rushen, 1986c, italics mine). However, a procedure in which the animal can *avoid* aversive stimulation is not an example of classical conditioning. The term 'avoid' implies that the behaviour of the animal determines whether or not aversive stimulation is presented (i.e. aversive stimulation is contingent on the animal's behaviour), consequently, it is an example of operant conditioning. Similarly, Dawkins (in press) describes the conditioned suppression procedure as follows: "an animal first learns that pressing a bar delivers food; then it learns that when a light comes on it will get an electric shock if it presses the bar". However, this is not the procedure involved in conditioned suppression, which involves presenting the aversive stimulus irrespective of whether or not the subject responds, i.e. true conditioned suppression is an example of classical conditioning. The procedure that Dawkins (1989) describes is an example of discriminative passive avoidance, in which the delivery of the aversive stimulus is contingent on the response and consequently is an example of operant conditioning.

Such confusion can, to some extent, be forgiven, given that much of the psychological literature itself uses inaccurate terminology (Davis, 1968), or does not adequately describe the procedure used in a particular experiment. In an attempt to overcome this confusion, the remainder of this section summarizes the principal differences between the aversion learning techniques.

There is only one truly classical aversive conditioning procedure - conditioned suppression. This involves the presentation of a conditioned stimulus (CS) which is followed by the delivery of an aversive stimulus. The aversive stimulus is delivered irrespective of the subject's behaviour i.e. the subject cannot avoid it. The remainder of the aversive conditioning procedures are examples of operant conditioning i.e. the behaviour of the subject does influence whether or not the aversive stimulus is delivered. Given that the subject can avoid further aversive stimulation, such procedures are known as avoidance techniques. The avoidance techniques can be sub-divided into two categories. Active avoidance requires the subject to perform a response in order to avoid i.e. it must be active in order to avoid. Passive avoidance requires the subject not to perform a certain response in order to avoid. Given that the response in question is effectively punished, this technique is also known as punishment. (However, arguments against the use of the term punishment are given in Chapter 8). Both active and passive avoidance techniques can be further sub-divided into locomotor and non-locomotor techniques, depending on whether or not the avoidance response involves the animal moving from one location to another. Active locomotor avoidance can be further sub-divided into one-way and shuttle avoidance, depending on whether the avoidance response is uni- or bi-directional (examples of shuttle and one-way avoidance tasks are given in Chapters 5 and 7). Finally, all of the avoidance techniques described so far can be sub-divided into signalled or unsignalled, depending on whether or not the subject is given a warning that, unless it performs an avoidance response soon or suppresses a punished response, the aversive stimulus will be delivered. The hierarchy of both classical and operant (i.e. avoidance) aversive conditioning procedures is summarized in Figure 3.1.

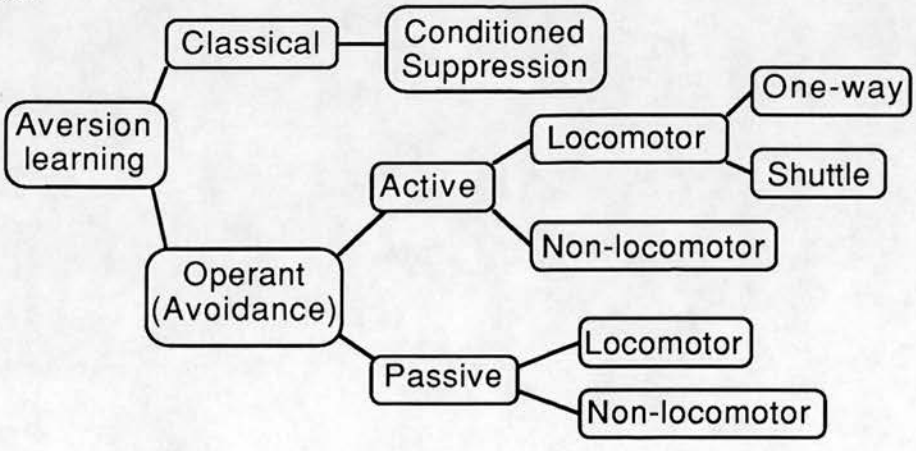


Figure 3.1. A summary of the aversion learning techniques. Note that the final level in the 'avoidance' hierarchy, namely signalled and unsignalled, is not shown.

3.2. Empirical validity

Given that conclusion reached in Chapter 2 was that the 'construct' validity of aversion learning techniques cannot be assessed, we can only assess their 'empirical' validity (Kerlinger, 1973). This involves testing the ability of the technique to differentiate between treatments of known degrees of aversiveness. Unfortunately, there is one major problem with this approach. The only way we can know the aversiveness of a given treatment is by measuring it. However, the only way we can validate our measure is by testing it with a treatment of known aversiveness. We therefore have a circular argument, a 'Catch 22'. Theoretically, it is impossible to overcome this problem. In practice it is only possible to validate the techniques by determining if they will discriminate between treatments which are *believed* to differ in their aversiveness. Unfortunately, a *belief* that a treatment either is or is not aversive is essentially a subjective judgement and is not a suitable basis for the scientific validation of a measure. However, physiological (and to some extent behavioural) indices of stress and fear could be used to add objective rigour to the validation process, by looking for correlations between different physiological measures of stress, fear and psychological measures of aversion.

A different approach to testing the empirical validity of psychological measures of aversion for the assessment of animal welfare was proposed by Rushen (1986c). He reviewed the psychological literature on aversion learning and used the effects of electric shock to assess the empirical validity of a variety of aversion learning techniques. However, there are a number of problems with such an approach. Firstly, the psychologist and the applied ethologist are essentially interested in different aspects of aversion learning. The psychologist is principally interested in learning, and aversive stimulation is simply one method of motivating the subject to learn. In contrast, one of the interests of the applied ethologist is the assessment of animal welfare, and consequently the applied ethologist is interested in the measurement of aversion. Learning is simply a means to this end. The psychologist can learn a great deal from studying learning at its limits and the failure to learn can be very informative. However, for the applied ethologist, learning failure results in a failure to measure aversion. The implications of learning failure for the assessment of animal welfare are discussed later in this chapter.

Rushen (1986c) also made the assumption that "electric shock of high intensity and/or long duration 'feels worse' than shock of low intensity and/or short duration". Although this "seems reasonable" (Rushen, 1986c), electric shock is a very unnatural stimulus and its use can sometimes give unpredictable results. For example, Fowler and Miller (1963) found that shocking the front paws of a rat reduced the speed with which it ran down a runway, whereas shocking the back paws resulted in an increase in the speed with which it ran down the runway. This raises the question of what the animal perceives is happening to it when it receives an electric shock? It is possible that the pain inflicted by a shock is similar to that which may occur when the animal is grasped either in the jaws or talons of a predator. However, the majority of potentially aversive husbandry procedures carried out in intensive systems do not actually cause the animal any pain. These procedures may be potentially aversive because they are seen by the animal as looming stimuli. Such looming stimuli may elicit a different set of defence reactions to those elicited by an electric shock, and this possibility is discussed further in Chapter 5. Therefore, although a review of the use of electric shock may be relevant for studies in which the husbandry procedure being evaluated actually involves the use of electric shock (e.g. electro-immobilization in sheep [Rushen, 1986b]), it may be unwise to generalize from the ability of techniques to discriminate between different intensities of electric shock to the ability to discriminate between different intensities of other frightening stimuli.

However, no matter what aversive stimulus is either being tested or used to assess the validity of a technique, the relationship between the intensity of the aversive stimulus, the level of aversion the animal experiences and the performance of the response associated with a given aversion learning technique must be considered. The following section does just this.

3.3. Stimulus intensity, aversion and response

Aversion is a subjective mental experience and as such cannot be observed directly. It is only possible to observe it indirectly through the effect it has on the animal's behaviour. Consequently, aversion is an intervening variable which cannot be measured directly and this has considerable implications for those interested in measuring it.

The presentation of a noxious stimulus to a subject causes it to experience the state of aversion. The relationship between the intensity of the noxious stimulus and level of aversion can be expressed as a function, f_1. The state of aversion can either cause the animal to perform some response in order to avoid

the stimulus, or cause the conditioned suppression of an operant response, and this 'response' is measured using one of the aversion learning techniques. The relationship between level of aversion and the 'response' can be expressed by a second function, f_2. However, the experimenter can only record the relationship between the intensity of the aversive stimulus and the 'response', f_3.

Figure 3.2 shows three examples of the possible relationships between stimulus intensity, level of aversion and the performance of the response. In all three examples, the relationship between stimulus intensity and response i.e. f_3, is linear. Obviously, if the functions f_1 and f_2 were both linear (Figure 3.2 a), then the resultant function, f_3, would also be linear. In such a case, the response that was measured would accurately reflect the level of aversion the subject experienced. Aversion could then be measured on an interval scale i.e. it could be measured on a continuous numerical scale, with, for example, one unit of aversion being half as aversive as two units of aversion.

However, the fact that the relationship between stimulus and response (i.e. f_3) is linear, does not necessarily imply that f_1 and f_2 are linear. For example, Figure 3.2 b shows a hypothetical situation where f_1 and f_2 are both curvilinear. In this case, when f_1 and f_2 are combined, the resultant function, f_3, is linear. However, f_3 does not accurately reflect the level of aversion that the subject is experiencing. In this example it underestimates the level of aversion at the intermediate intensities of the aversive stimulus. In such a case, the level of aversion can no longer be measured on an interval scale. However, it can still be measured on an ordinal scale i.e. various treatments can be ranked according to their aversiveness.

However, Figure 3.2 c shows an example where the relationship between stimulus intensity and level of aversion is non-monotonic i.e. the function is characterized by at least two phases, one of which has a negative slope. In this example, aversion can not be measured on either an interval or an ordinal scale.

Strictly speaking, given that it is impossible to determine the nature of the two functions relating stimulus intensity with level of aversion and level of aversion with stimulus intensity, *it is impossible to measure aversion.* However, if it is assumed that the two functions are linear (as in Figure 3.2 a), then aversion can be measured on an interval scale. However, given that many biological functions are non-linear (e.g. growth, enzyme activity and learning are all non-linear functions) it is unlikely that functions relating a stimulus, a mental state and a response would be exactly linear. Given that it is impossible to prove that these functions are linear, aversion *cannot* be measured on an interval scale.

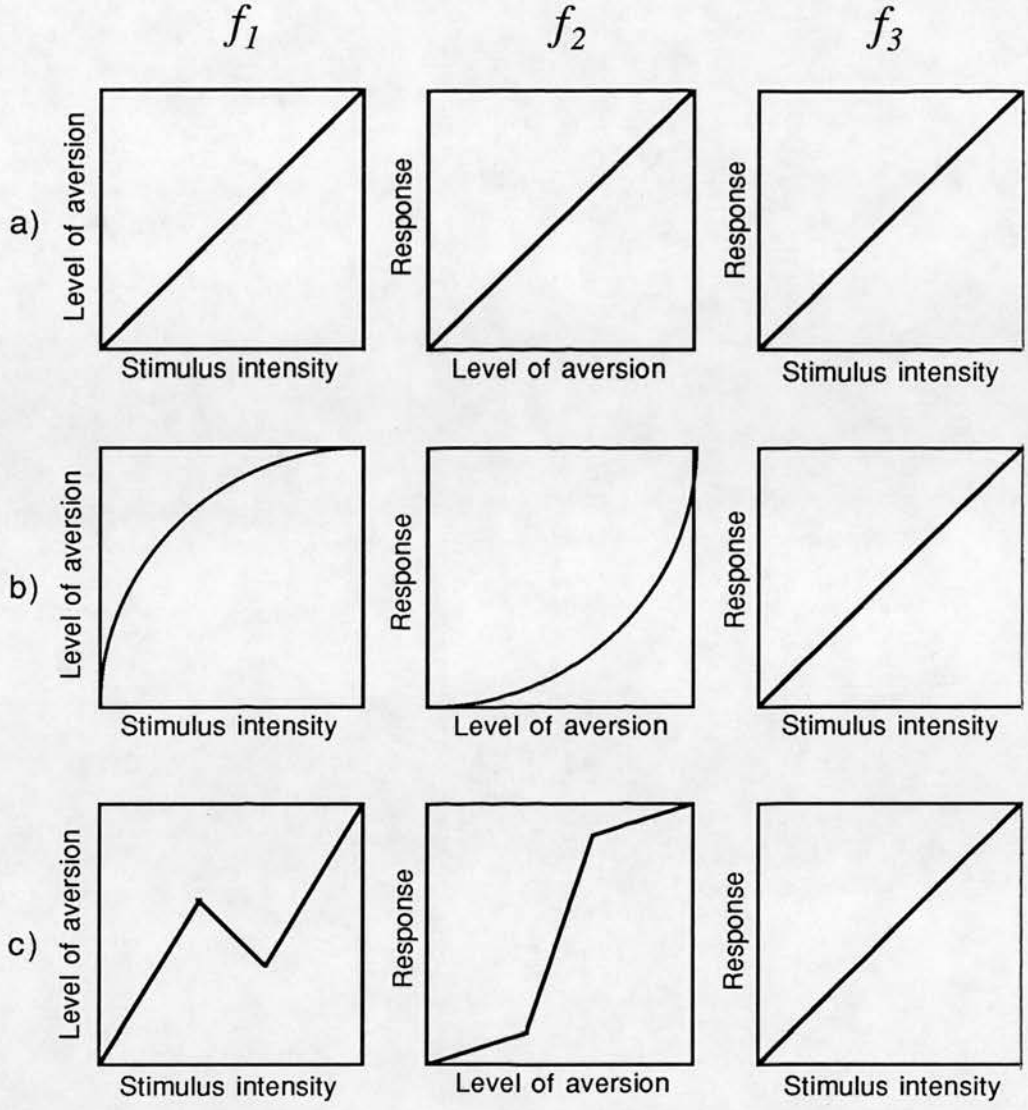


Figure 3.2. Three hypothetical relationships between stimulus, aversion and response.

Alternatively, if it is assumed that the two functions are monotonic (but not necessarily linear, as in Figure 3.2 b), then aversion could be measured on an ordinal scale. However, is this a reasonable assumption? It is unlikely that an increase in the intensity of a stimulus would result in an increase in aversiveness, followed by a decrease in its aversiveness (or vice versa for that matter)[1]. It is, of course, impossible to prove that the function relating stimulus intensity and level of aversion cannot be non-monotonic, it is simply that common sense suggests that

[1] It is important to differentiate between increasing intensity and an increasing number of exposures to an aversive stimulus. Increasing the number of exposures to a stimulus will probably result in habituation to the stimulus (discussed later), and such a process could be a non-monotonic function.

this would be unlikely. However, the function relating level of aversion and response possibly could show a non-monotonic function. For example, the animal may initially show an increase in response as a result of increasing levels of aversion. At very high levels of aversion, the aversion may interfere in some way with the animal's ability to respond e.g. it may freeze. Indeed, there appears to be an inverse relationship between shuttle avoidance and the intensity of the electric shock used as the aversive stimulus (Theios, Lynch and Lowe, 1966; McAllister, McAllister and Douglas, 1971). The rejection of the assumption that the two functions are monotonic means that it is impossible to measure aversion, even on an ordinal scale.

Given that the use of aversion learning techniques as measures of aversion is therefore based on an assumption which cannot be proved scientifically, the use of physiological measures might appear more attractive. Physiological techniques can measure the stress response on an interval scale. However, given that animal welfare is about how an animal 'feels' about its environment and the procedures to which it is subjected (Duncan and Petherick, 1989), physiological techniques suffer from exactly the same problem i.e. that it is impossible to determine the function relating the physiological measure of stress and how the animal 'feels' e.g. the level of aversion it experiences. Just as the function relating stimulus intensity and level of aversion is probably non-linear, so too the function relating the physiological measure of stress and how the animal feels is likely to be non-linear. Consequently, the fact that we can measure physiological variables on an interval scale does not mean we can measure how an animal feels on an interval scale. Indeed, the function relating the physiological measure and the animal's 'feelings' could be non-monotonic and, consequently, physiological measures cannot be used to assess animal welfare either.

This places the scientist in a difficult situation. There is a clear need for an objective means of assessing animal welfare (e.g. Command Paper 2836, 1965). However, an attempt to do so violates scientific principles. There are, therefore, two alternatives. Either we give up our attempts to assess welfare or we make some assumptions which cannot be tested scientifically. Of the two alternatives, I prefer the latter. Therefore, this study assumes that the functions relating stimulus intensity, level of aversion and response are monotonic. Consequently, aversion can be measured on an ordinal scale i.e. the aversion learning techniques can be used to rank treatments and procedures in the order of their aversiveness.

3.4. Variability of aversion learning

In the early years of experimental psychology, there appeared to be no limit to the behaviour which could be conditioned, and this period was one of "heroic optimism, characterized by a belief in the possibility of constructing a comprehensive theory of behaviour" (Hinde, 1973). However, in the early 1960s it started to become apparent that some associations could not be acquired as readily as others.

3.4.1. "The misbehaviour of organisms"

One of the first reports of some tasks being difficult or even impossible to condition came from Breland and Breland (1961). The Brelands had originally been impressed with a demonstration of conditioning given by Skinner.

> "The pigeon was to send a wooden ball down a miniature alley towards a set of toy pins by swiping the ball with a sharp sidewards movement of the beak...The spectacle so impressed Keller Breland that he gave up a promising career in psychology and went into the commercial production of behaviour" (Skinner, 1958).

However, the Brelands soon encountered a number of problems, reported in their famous paper entitled "The misbehavior of organisms" (Breland and Breland, 1961). The paper includes a number of examples, including one, which is often cited, in which a pig had been trained to collect large wooden 'coins' and deposit them in a 'piggy bank' in return for a food reward. The pig quickly acquired the response and initially performed the response "eagerly". However, over a number of weeks the response became slower and slower, with the pig dropping the 'coins', rooting them, picking them up and tossing them about before eventually placing them in the 'bank'. Although such behaviour was not rewarded and even acted to delay the delivery of the food reward, the behaviour persisted and even gained in strength, to such an extent that the pig did not receive sufficient food to meet its daily intake requirement. This problem developed repeatedly in successive pigs and other species developed similar "misbehaviour" problems in other relatively simple operant tasks. According to the contemporary behaviourist theories of that time, such misbehaviour simply should not happen. Acknowledging this, the Brelands accounted for such "misbehaviour" with what they termed "instinctive drift"; the process by which "learned behaviour drifts towards instinctive behaviour" when ever the animal's instinctive behaviour is similar to the response being reinforced.

It was not until 1966 that the notion that all stimuli were equally associable with all responses was finally refuted. Garcia and Koelling (1966) demonstrated that an association could be learnt between two particular CSs and two particular USs i.e. CS1→US1 and CS2→US2, but the crossover associations i.e. CS1→US2 and CS2→US1 could not be learnt. They first trained a group of rats to drink from a drinking tube which caused the presentation of a noise and flashing lights. This was achieved by placing an electrode in the drinking tube which switched on the lights and the noise when it was touched by the rat's tongue. Drinking this 'bright noisy water' then resulted in the delivery of a brief electric shock i.e. the rat was punished. The rats soon learnt to stop drinking the 'bright noisy water'. Similarly, a second group learnt to stop drinking saccharin flavoured water which was punished by making the rats ill (either with an injection of lithium chloride or being exposed to X-rays). However, a third group failed to show any aversion to 'bright noisy water' when it was associated with illness, and a fourth group failed to learn an association between saccharine flavoured water and the delivery of an electric shock. Therefore, the rats could learn the association lights & noise→electric shock and saccharin→illness, but could not learn the association lights & noise→illness or saccharin→electric shock. Garcia and Koelling's (1966) conclusion was simply that some things are more "learnable" than others.

3.4.2. Constraints on avoidance learning

Early avoidance studies usually only reported results from subjects which learnt to perform the avoidance task. Latterly, experimenters have admitted that many subjects fail to learn the given task in some avoidance techniques (Bolles, 1970, 1971). For example, even after training for hundreds of trials on a signalled, lever-press avoidance task, rats avoided shock on less then 20 per cent of trials (Biederman, D'Amato & Keller, 1964). Pigeons can only be taught to peck a key to avoid shock after extensive and elaborate shaping (Hineline & Rachlin, 1966). Jacobs and LoLordo (1980) reported that "as many as one third of the rats originally scheduled as subjects failed to acquire the wheelturn avoidance response".

Just as certain 'avoidance' responses do not increase in frequency even when associated with an avoidance contingency, certain responses do not decrease in frequency when punished. For example, Shettleworth (1978) demonstrated that, although punishment of scrabbling behaviour in hamsters resulted in a decrease in the frequency of that behaviour, punishment of face washing resulted in an increase in the frequency of that behaviour. Similarly, responses which are elicited by

aversive stimulation (e.g. aggression, certain defence reactions) appear to be facilitated by punishment (Morse, Mead and Kelleher, 1967; Melvin and Anson, 1969; Walters and Glazer, 1971; Melvin and Ervey, 1973).

3.4.3. Biological constraint theory

The discovery of such constraints on learning lead to a shift away from learning principles and general-process laws of conditioning to more biologically oriented theories of learning. One such theory was Bolles' (1971) 'species-specific defence reaction' (SSDR) hypothesis of avoidance learning which was introduced in Chapter 2. This was based on the fact that, as described earlier, certain avoidance responses were not acquired very readily. Bolles (1971) argued that the reason for this was that aversive stimulation restricted the subject's behavioural repertoire to a subset of innate defensive responses. Consequently, if the required avoidance response did not lie within this subset of behaviour, the behaviour would not be expressed and so could not be acquired as an avoidance response. In contrast, if the avoidance response was one of the animal's innate defence reactions it would be expected to be acquired as an avoidance response.

Recently, biological constraint theories have been criticized. As Damianopoulos (1989) points out, the biological constraint theories are based on negative data i.e. the failure to learn. In recent models of scientific explanation negative data are no longer considered to be sufficient to falsify a theory or hypothesis (e.g. Grunbaum, 1969; Hesse, 1974). Consequently, Damianopoulos (1989) concluded that the "evidence used to support inferences of biological constraints indicates that the evidence is insufficient to warrant inferences of biological constraints operating as mechanisms to hinder or facilitate learning".

Domjan (1983) reached a similar conclusion in a case-by-case review of the supposed examples of biological constraints. For example, Domjan (1983) accounted for the misbehaviour of Breland and Breland's (1961) pigs in depositing coins for a food reward as reflecting "performance factors rather than a limitation on association learning". He suggested that such misbehaviour resulted from a conflict between the instrumental and classical associations inherent in the experiment. The instrumental contingency required the pigs to release the coins. The classical contingency arose from pairings of the coins and food. However, as an experiment by Timberlake, Wahl and King (1982) showed, the classical contingency did not follow the traditional stimulus-substitution view of classical conditioning. They trained rats to deposit ball bearings in a hole for a reward. The rats developed a similar 'misbehaviour' to that shown by the Brelands' pigs.

However, the responses towards the ball bearings were far more time consuming and elaborate than those towards food pellets. (The stimulus-substitution view would predict that the responses towards the ball bearings would be very similar to those towards the food pellets.) Consequently, Domjan (1983) suggested that the ball bearings elicited responses that were part of the rat's innate appetitive behaviour repertoire. A similar argument can be used to account for the failure of some animals to learn certain avoidance responses. Again, this could arise from the conflict between instrumental tendencies to avoid (e.g. move into the other half of a shuttle box) and the classical elicitation of natural defence responses (e.g. freezing).

However, the fact remains that, for whatever reason, animals either cannot acquire certain tasks, or acquire them very slowly. This problem has considerable implications for the application of aversion learning techniques in the assessment of animal welfare and these are considered in the following two sections.

3.5. Implications of failure to learn

Before discussing the implications of learning failure, it is first necessary to consider how aversion learning techniques will be used in the assessment of animal welfare. I therefore wish to propose the following approach to welfare assessment.

Domestic animals are exposed to a wide range of commercial husbandry procedures. The nature of some of these procedures are such that they are probably aversive to some animals. One of the principal aims of welfare research and subsequent welfare legislation is therefore to determine which procedures are so aversive that they should be prohibited by law. The first stage in this process would be to select an upper threshold of aversion. Any procedure which resulted in levels of aversion above this threshold would be considered to be too aversive and would, therefore, be prohibited. However, in any population, different animals would probably show a wide range of levels of aversion to any one procedure. Whilst the majority of animals may not find a procedure particularly aversive, a few may find it very aversive. If a treatment was to be prohibited if *any* subject showed levels of aversion above the threshold, all but the most innocuous of treatments would probably be banned. Therefore, for a given treatment to be prohibited, a proportion of the subjects tested would have to show levels of aversion above the threshold. Parliament could then use the available scientific evidence to determine the exact values of the aversion threshold and proportion of subjects, and incorporate these values into the welfare legislation. For example, Figure 3.3

shows two treatments, a and b, which cause different levels of aversion. Only a very small proportion of subjects show levels of aversion above the threshold, in response to treatment a. Assuming the proportion was less than that stipulated in the legislation, this treatment would not be banned. However, a large proportion of animals show levels of aversion above the threshold in response to treatment b, which would, therefore, be prohibited.

Such an approach clearly involves measuring aversion in a sample of animals which is representative of the population as a whole. However, if a number of subjects failed to learn the task required in a given aversion learning technique, their level of aversion could not be recorded. If the failure to learn was not affected by the level of aversion the subject experienced, this would be of little consequence to the validity of the study, because the sample would still be representative of the population. However, it is possible that the level of aversion would affect learning performance. It is possible that the levels of aversion in the animals that did not learn were so low that the animals were not motivated to learn, or that they were so high that they imposed a constraint on the animals' learning ability. It would be impossible to determine whether the failure to learn was due to either high or low levels of aversion. Consequently, the study would have to be abandoned because the remaining group would no longer be representative of the population as a whole and it would be impossible to tell whether the recorded levels of aversion were either under- or over-estimating the level of aversion experienced by the population as a whole.

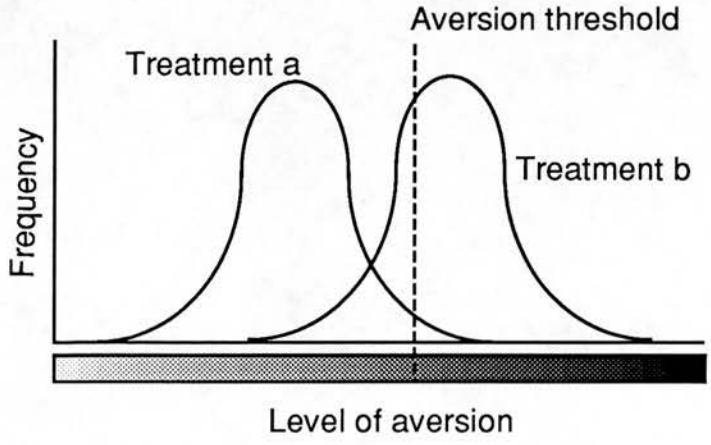


Figure 3.3. Two hypothetical distributions of aversion levels resulting from two treatments, a and b. See text for an explanation of the aversion threshold.

3.6. Implications of slow learning

It is possible that all subjects would eventually learn a task given extensive training over a considerable number of trials. However, continued exposure to a stimulus eventually leads to habituation (Thompson and Spencer, 1966; Hinde, 1970). The more a subject is exposed to an aversive stimulus, the less aversive that stimulus becomes. Generally, it takes an animal longer (either in terms of number of exposures or duration of exposure) to habituate to a more aversive stimulus than to a less aversive one. Indeed, this is could be used as measure of aversion. However, the animal may require very extensive exposure to a highly aversive stimulus before it showed any signs of habituation. Consequently, the measurement of aversion itself could be highly stressful and habituation can be rejected as a possible measure of aversion on ethical grounds.

In the context of aversion learning techniques, the gradual reduction of aversion as a result of habituation can confound the experimental treatment. For example, two subjects both experience the same level of aversion towards a given treatment. In an attempt to measure this level, both are subjected to one of the aversion learning techniques. One subject learns the task quickly and given that it receives minimal exposure to the aversive stimulus, it has little chance to habituate to it. Consequently, the stimulus is still very aversive, causing, for example, a high degree of operant suppression. The other subject is slow to learn and habituates to the aversive stimulus before it learns to avoid it. Consequently, the subject will show a relatively low level of aversion towards it, causing relatively little operant suppression. Although both animals initially experienced similar levels of aversion, the aversion levels we eventually measure for each subject are different.

Clearly, any aversion learning technique which is used as a measure of aversion in the assessment of animal welfare must be learnt after relatively few exposures to the aversive stimulus.

3.7. Criteria for a measure of aversion

The preceding discussion suggests a number of criteria which need to be met before an aversion learning technique can be used as a measure of aversion in the assessment of animal welfare. These criteria are as follows:

i) It should be learnt by all of the subjects tested. This would ensure that the subjects tested were representative of the population as a whole.

ii) It should be learnt with minimal exposure to the aversive stimulus. This would ensure that the subjects would not habituate to the aversive stimulus before the level of aversion caused by the stimulus could be measured.

iii) It should be able to discriminate between different levels of aversion.

iv) The technique itself should not be so stressful to the animal that its use might be questioned on ethical grounds.

3.8. Summary

There are clearly a number of pitfalls waiting to trap the unwary applied ethologist who wishes to use aversion learning techniques in the assessment of animal welfare. Ideally, the various aversion learning techniques should be assessed using both the species and typical treatments under investigation i.e. before using such techniques to assess of the aversiveness of husbandry procedures to laying hens, the technique should be validated using hens as experimental subjects and one (or more) of the husbandry procedures as the (potentially) aversive stimulus. The aim of the current study was to do just this i.e. determining which, if any, of the aversion learning techniques can be used to assess the aversiveness of looming stimuli to domestic hens.

CHAPTER 4 Development of an Operant System

4.1. Introduction

Operant conditioning requires the experimental subject to learn an association of the form response → reinforcement. In the simplest case, every response is reinforced. However, it is more usual to arrange reinforcement on some schedule, so that, for example, every fifth response is reinforced. An operant system must therefore be able to:

i) record a response;
ii) to deliver the reinforcer;
iii) control the schedule linking response and reinforcer.

Much of the early work on operant conditioning used the pigeon as an experimental subject (Ferster and Skinner, 1957). Given the obvious similarities between the pigeon and the domestic hen, it was decided to base our operant system on that developed by Ferster and Skinner.

4.2. The operant hardware

The operant hardware can be divided into two distinct components: some means of recording a response, and some way of delivering reinforcement to the subject.

4.2.1. Recording the response

The nature of the response chosen for operant conditioning is mainly dependent on the species being tested. The animal should have full control over the performance of the response and should be able to perform it repeatedly. It has been shown that for an operant response to be readily required, it should be appropriate to the reinforcer (e.g. Shettleworth, 1975) for example pecking for a food reinforcer or running away from an aversive reinforcer. The peck of a bird is,

therefore, well suited to operant conditioning and was first used by Skinner (1948). He trained pigeons to peck at a plastic disc which he termed the key. Each peck broke an electric circuit allowing the response to be recorded. Given the considerable improvement in electronics since 1948, it was possible to design a new operant key (Figure 4.1). The mechanical switch was replaced with a slotted opto-switch. This was comprised of an infra-red source and sensor housed in a slotted moulding. A peck at the armature caused an aluminium block attached to the armature to move into the slotted opto-switch. This caused a break in the infra-red beam which was detected by the sensor in the slotted opto-switch. As the circuit could be made and broken without the use of physical contact, the life of the key (in terms of number of operations) was considerably extended.

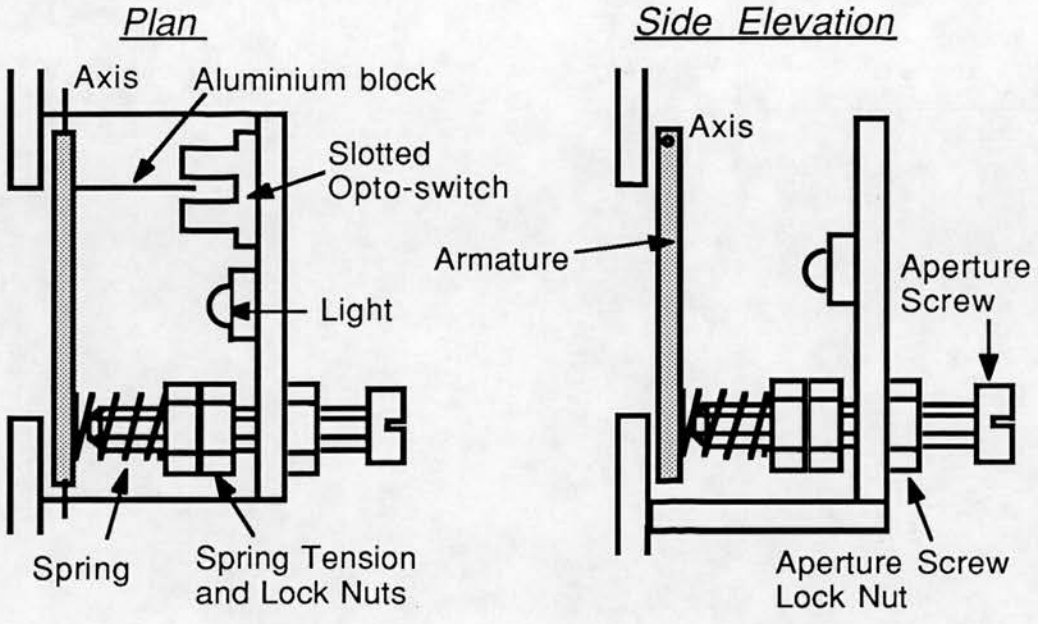


Figure 4.1. The improved operant key.

The key excursion was limited by the aperture screw. The key excursion could be set to the required size by adjusting the aperture screw, and then locked by tightening the aperture screw lock nut. The spring ensured that the armature returned to its original position. The force required to operate the key could be altered by adjusting the spring tension, which could be adjusted using the spring tension nut on the screw. Once the spring tension had been set, it could be locked by tightening the spring tension lock nut. The armature was illuminated from behind by an 'ultra-bright' light-emitting diode, which has a longer life and uses less power than a traditional light bulb.

The new key worked well when tested. However, it would occasionally record a number of 'responses' from one peck. Examination of the opto-switch output with an oscilloscope (Figure 4.2) revealed that the switch was prone to 'bounce' for a fraction of a second after the peck. If this bounce crossed the computer threshold it was recorded as another response. The problem was solved by programming the computer to disregard any 'responses' with an inter-response interval of less than 70ms. As this interval was much less than the minimum inter-response interval a bird was capable of achieving, it ensured that the only those 'responses' due to switch bounce were filtered out.

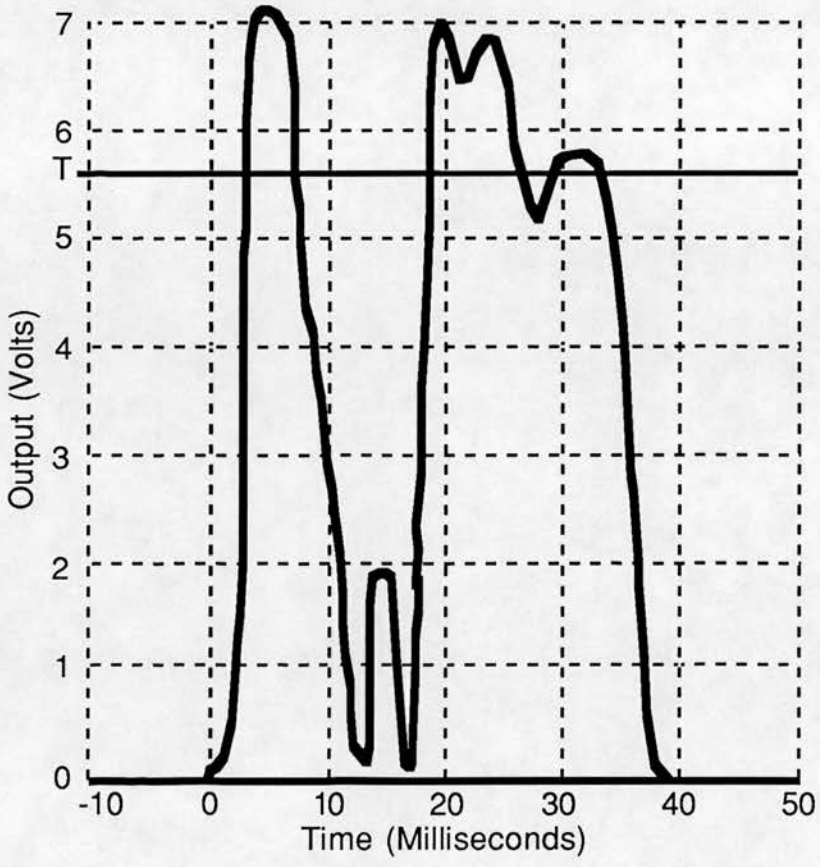


Figure 4.2. A typical output trace from the operant key when it was pecked once. The threshold above which the computer records a response is marked T. The minimum inter-response interval of 70ms (see text) ensured that this was recorded as one and not three responses.

4.2.2. Delivering reinforcement

The reinforcer chosen for operant conditioning must be of some motivational significance to the animal being tested, that is, it should act so as to satisfy at least one of the animal's current motivational requirements. Although a range of

events have been found to act as operant reinforcers, the most widely used has been the delivery of food to a hungry animal. It is a relatively simple task to ensure that a subject is motivated to feed by depriving it of food for a given period prior to testing. The subject can then be reinforced by being given access to food. With the pigeon, this has traditionally been achieved by raising and lowering a food tray (e.g. Ferster and Skinner's food delivery system is shown in Figure 4.3). The bird was given access to the food by activating a solenoid which raised the food tray allowing the bird to feed from it. At the end of the reinforcement period, the solenoid was switched off and the food trough dropped out of reach of the subject. Reinforcement was usually signalled by switching on a light as the food tray was raised.

Unfortunately, although there have been attempts to use this design with domestic fowl, these were largely unsuccessful (I.J.H.Duncan, pers. comm.). Firstly, the domestic hen is larger than a pigeon, and consequently has a greater food intake. This requires the use of a larger food tray which would be too heavy to lift with a standard solenoid. Secondly, the operant panels were to be used in commercial battery cages and had to give the birds access to the standard battery food trough. It was therefore decided that access to the food should be controlled by opening a small door through which the bird could feed.

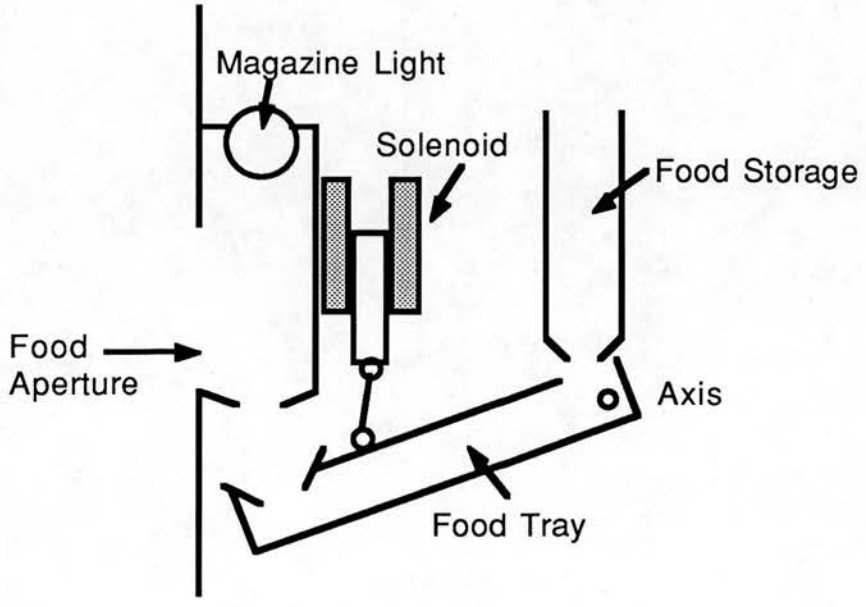


Figure 4.3. Ferster and Skinner's original food delivery system.

In prototype I (Figure 4.4) the door was pulled open by a solenoid. The door was closed by switching off the solenoid, which allowed the door to swing shut

under its own weight. A solenoid-operated latch prevented the door being pushed open by the bird. When this prototype was tested, a serious flaw in the design was discovered. If the bird kept its head in the doorway as the door swung closed, the door did not latch, allowing the bird to subsequently push open the door and feed. In an attempt to cure this problem, lead weights were attached to the bottom of the door so as to increase its mass. This extra mass was too great for the solenoid to lift, resulting in it overheating and failing.

Prototype II (Figure 4.4) attempted to overcome these problems by attaching the door directly to a stepper motor. The door could be rotated open by sending a given number of positive pulses to the motor, and closed by sending the same number of negative pulses. This ensured that, unlike prototype I, the door was both opened and closed with a positive action i.e. the bird was effectively pushed away from the food. However, over a large number of trials the exact position of the stepper motor axle tended to drift. Consequently, the door either did not close fully or the motor continued to rotate the door after it had made contact with the frame, resulting in the motor overheating and failing.

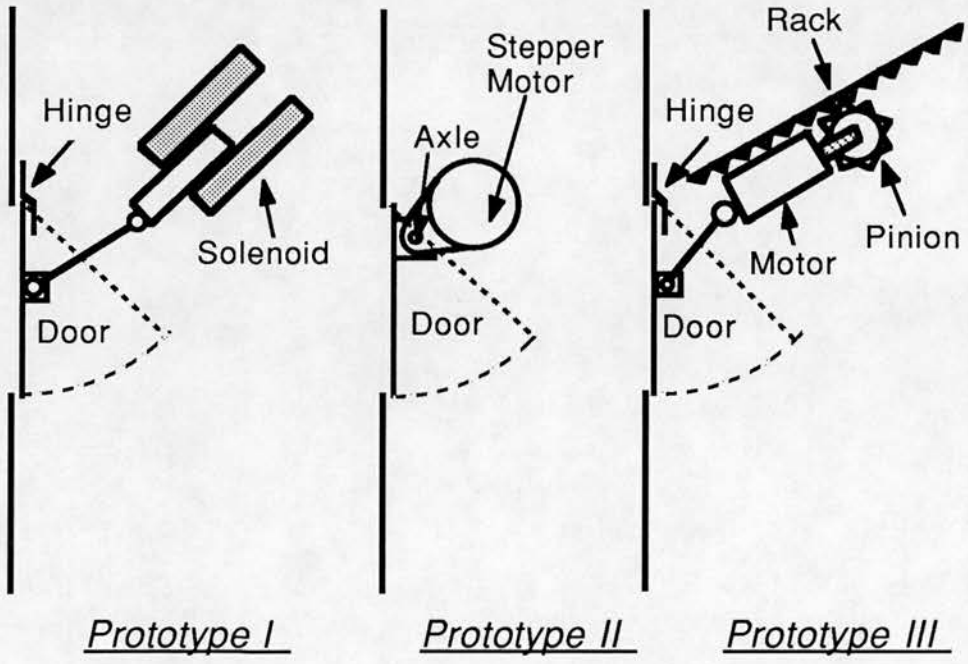


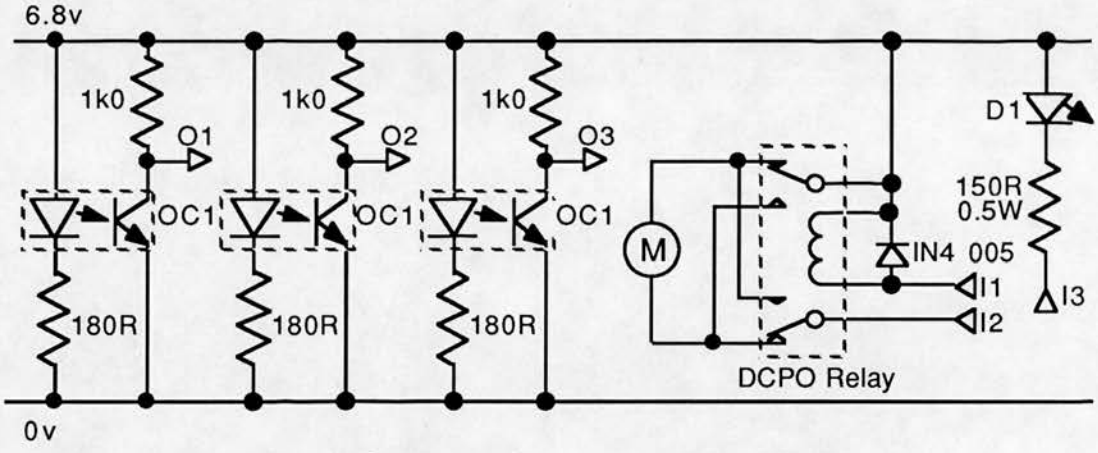
Figure 4.4. The three prototype food access control systems.

Prototype III (Figure 4.4) aimed to combine the best features of the first two prototypes. The door was pulled open and pushed closed by a motor mounted on a fixed rack. Slotted opto-switches mounted at either end of the rack detected when

the motor had opened or closed the door. These were originally connected in series to one input channel on the computer which controlled the system. The motor was then activated until either one was broken. However, this prevented the system from determining whether the door was open or closed, and the two were, therefore, connected to two separate input channels. This allowed the computer to ensure the door was closed when the control program was first executed. This minor change resulted in a food access control mechanism which was very reliable.

4.2.3. The final hardware configuration

The key and prototype III door were combined on a single panel (Plate Ia), and the circuit diagram for the complete panel is shown in Figure 4.5. The circuit has three outputs; the key switch and the two motor end switches. It also has three inputs; one switches the key light on and off, one controls the supply of power to the motor, and one switches the polarity of the supply to the motor (hence determining its direction) by switching the change-over relay.



OC1	Opto-switch (RS 306-061)	D1	LED (RS 588-623)
O1	Key switch	I1	Motor direction
O2	Upper motor end switch	I2	Motor power
O3	Lower motor end switch	I3	Key light

Figure 4.5. The circuit diagram of the operant panel.

Originally, operant systems were controlled by a collection of relays and timers, and results recorded on chart recorders (Ferster and Skinner, 1957). However, this control and recording task is now ideally suited to implementation by a microcomputer. An Acorn/BBC model B+128 microcomputer was chosen for this particular implementation. It was interfaced to the operant panels via a Paul Fray interface system connected to the 1MHz Bus. This gave a total of 32 digital

channels, each of which could be configured as either an input or an output. Given that each panel required a total of six channels, it was possible for the one computer to control up to five panels.

Although the ultimate destination for the record of responses and reinforcement was a floppy disc, accessing the disc whilst the system was running resulted in a considerable reduction in the response time of the system. Therefore the four 16 kilobyte sideways random access memory (RAM) banks on the BBC microcomputer were configured as a continuous data buffer. The use of a compact data format allowed approximately 20,000 records to be stored before the buffer was full. This was sufficient to store data from four panels for at least a 24 hour period, and as a result the buffer had only to be transferred onto disc once a day.

4.3. Schedules of reinforcement

Before describing the development of the control and recording software, it is first necessary to describe the different schedules of reinforcement which can be used to determine when reinforcement is delivered. The simplest schedule is continuous reinforcement (CRF), which simply involves reinforcing every response that the subject performs. However, given that each response is reinforced with food, the subject can quickly gain sufficient food to satisfy its hunger and it usually then stops performing the operant response. CRF is, therefore, usually only used when the subject is being taught to perform the operant response. Once the subject has learnt the operant response it is usually trained to respond on higher schedules of reinforcement. The simplest of these is known as fixed ratio (FR). This involves the subject being reinforced for performing a fixed number of responses. For example, an FR5 schedule reinforces the subject after every fifth response. Note that CRF is, therefore, the same as FR1.

Variable ratio (VR) schedules reinforce the subject after a variable number of responses. The actual number of responses required is given as the mean number (n) of responses the subject has to perform, with the actual number falling between 1 and $2n$-1. Note that a different random number is selected after each reinforcement e.g. on a VR10 schedule the subject may have to perform six responses for the first reinforcement, 18 for the second, one for the third, 11 for the fourth etc. Traditional operant systems would use a continuous paper tape loop to store the sequence of random numbers. Consequently, the same sequence of numbers would be used again once the tape had gone full circle. Providing the tape loop contains a sufficient number of random numbers, there was little chance of the subject learning the sequence (Ferster and Skinner, 1957).

The other common schedules of reinforcement are the interval schedules. Fixed interval (FI) reinforces the first peck to occur after some given time interval after the previous reinforcement. Although the value of interval schedules of reinforcement was traditionally given in minutes, the operant control program listed in Appendix I defines interval schedules in terms of seconds. Therefore, a FI60 second (equivalent to the traditional FI1) schedule gives the subject reinforcement immediately after the first response to occur 60 seconds after the previous reinforcement. Variable interval (VI) schedules are similar to FI schedules, except that the interval before reinforcement is ready to be delivered is randomly varied (in a similar way to the ratio value is in VR schedules). For example, a VI60 second schedule will reinforce the first peck after an interval of between 1 and 119 seconds.

Each of the four simple schedules (i.e. FR, VR, FI and VI) result in different operant performance characteristics (Reynolds, 1968), and these are summarized in Figure 4.6. On a FR schedule, the subject typically pauses after each reinforcement, before responding at a steady rate until the next reinforcement is delivered. On a VR schedule, this post-reinforcement delay is not seen, and the subject starts to respond at a high rate immediately after each reinforcement. The FI schedule is characterized by a "scallop" i.e. the response rate slowly increases after each reinforcement until the subject receives the next reinforcement. The VI schedule, like the VR schedule, results in the subject performing the operant response at a high rate immediately after each reinforcement.

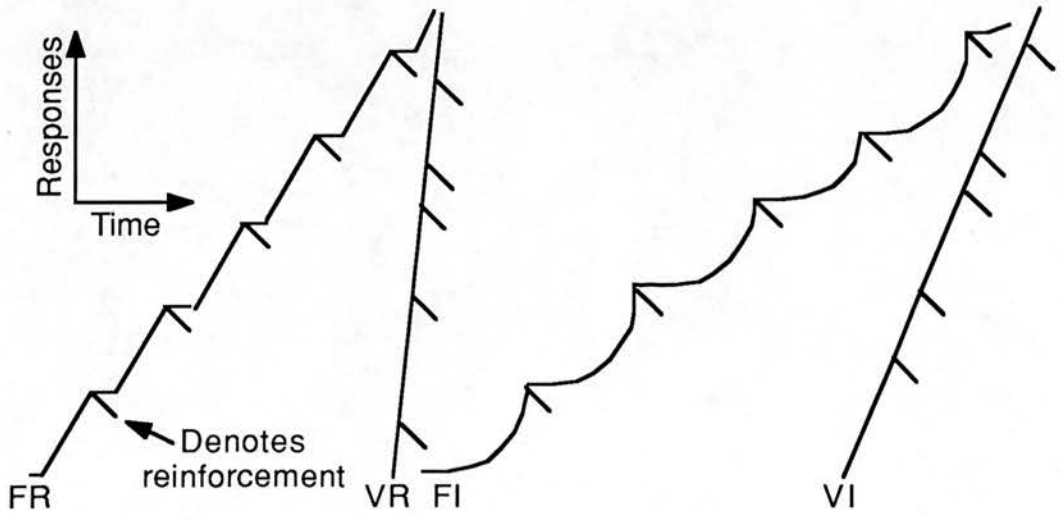


Figure 4.6. Typical performances associated with the four simple reinforcement schedules. (After Reynolds, 1968.)

4.4. The control and recording software

The control and recording software was written in BBC BASIC and used the Paul Fray 'Spider' real-time control extensions. This high level interpreted language had both the power and speed required to control a complex operant system. Appendix I gives a listing of a complete operant control program, and a detailed description of this program is given below. The program can deliver reinforcement under any one of the four simple schedules i.e. fixed ratio, variable ratio, fixed interval or variable interval (interval schedules are specified in seconds). Note that in the following sub-sections, any references to procedures or variables used by the program are set in a different font (i.e. `Apple Courier`) to that used for the main text (i.e. Times Roman).

4.4.1. The main program

The program first executed `PROCinit` which initialised all the variables, including the schedule type, which was split over two flags; `ratio` and `fixed`. After printing the program title and schedule type, the operant key was activated by calling `PROCon`. This set up a pipe[1] to call `PROCkey_peck` whenever the key was pecked.

`PROCon` also initialised the appropriate schedule, depending on the value of the flag `ratio`. If `ratio` was true, `PROCset_ratio` set `reward_count` to the value of the current key peck count (`key_count`) plus an increment. The increment was calculated by `FNinc(`*value*`)`, which simply returned its parameter *value* if the schedule was fixed, otherwise returned a random integer between one and twice the *value* minus one. If `ratio` was false, `PROCset_interval` set the flag `interval_over` to false to indicate that the interval had not yet expired. It then set up a timer pipe for the duration of the interval, which was calculated by `FNinc`. When this timer had expired, `PROCint_over` set the `interval_over` flag to true, ensuring that the next peck was reinforced.

The program then entered the `WAIT` state; it essentially 'waited' for the occurrence of any event for which pipes had been set. When an event occurred (for example the key being pecked), it called the appropriate procedure to handle that event.

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[1] A 'pipe' is the term Paul Fray use to describe a call to an event-handling routine. A pipe is denoted by the character "|". For example, the following statement `|(SWITCH 1, ON) PROCon` sets a pipe to call the procedure `PROCon` whenever the input on channel 1 is switched on.

PROCon set a second pipe which called PROCoff when function key 0 was pressed. This terminated all of the pipes, which resulted in the WAIT statement itself terminating. Control then passed to PROCfile which saved the data buffer on to a floppy disc before the program stopped.

4.4.2. Handling key pecks

Whenever a key was pecked, PROCkey_peck first checked to ensure that the interval between this response and the previous response was greater than the minimum inter-response interval. This ensured that any 'responses' due to key 'bounce' were not processed as key-pecks. If the key light was out, the peck should not have been reinforced, and so the routine terminated by calling PROCbad_key, which saved a 'bad' key record. Otherwise, the response was saved as a 'good' peck; the current time was printed on the display, and the routine called either PROCratio or PROCinterval to determine if reinforcement should be delivered.

PROCratio delivered reinforcement if the current key count was equal to (or greater than) the key count which was to be rewarded (held in the variable reward_count). PROCinterval delivered reinforcement if the peck occurred after the interval timer had expired (i.e. interval_over was true).

4.4.3. Controlling food access

Reinforcement was delivered by calling PROCopen. This set a pipe which called PROCstop_open when the upper motor end-switch was activated. The motor direction line was set to open the door, and the motor power line was switched on. This started the door opening. The 'door open' event was then saved; the current time was printed on the display; and, the flag open was set to true. (This flag was used by PROCoff to ensure the system was not stopped whilst the door was open.)

When the motor hit the upper end-switch, PROCstop_open switched off the motor power and motor direction lines, and set a timer pipe to close the door after an interval of sec_reward seconds. When this interval was over, PROCclose set a pipe to call PROCstop_close when the lower end-switch was activated, before switching on the motor power. PROCstop_close switched off the motor power, set either the new interval or ratio value (depending on the current schedule type), and finally set the open flag to false.

4.4.4. Data storage

Originally, operant responses were recorded on a cumulative recorder (Figure 4.7). This consisted of a roll of paper which slowly unrolled under a pen as time passed. Each response the subject performed caused the pen to move up one unit towards the top of the paper. When the subject received reinforcement, the pen was briefly moved down and back a short distance. This caused a mark on the cumulative record, allowing the easy identification of a reinforcement on the trace. Once the pen reached the top of the paper, it jumped back to the bottom of the page, ready to move back up the page whenever the subject responded.

Given that important features on a cumulative record do not usually have any absolute starting points with respect to either time or number of responses, cumulative records are usually presented without axes. The scale used in the record is usually denoted by a rectangle, the horizontal and vertical length of which shows the scale of the time and number of responses respectively. The slope of a cumulative record is equivalent to the rate at which the subject performed the operant response, and the rectangle denoting the scale usually contains a number of lines of different slopes which represent a selection of different response rates. Figure 4.8 shows a typical cumulative response record and the rectangle used to denote the scale of the record.

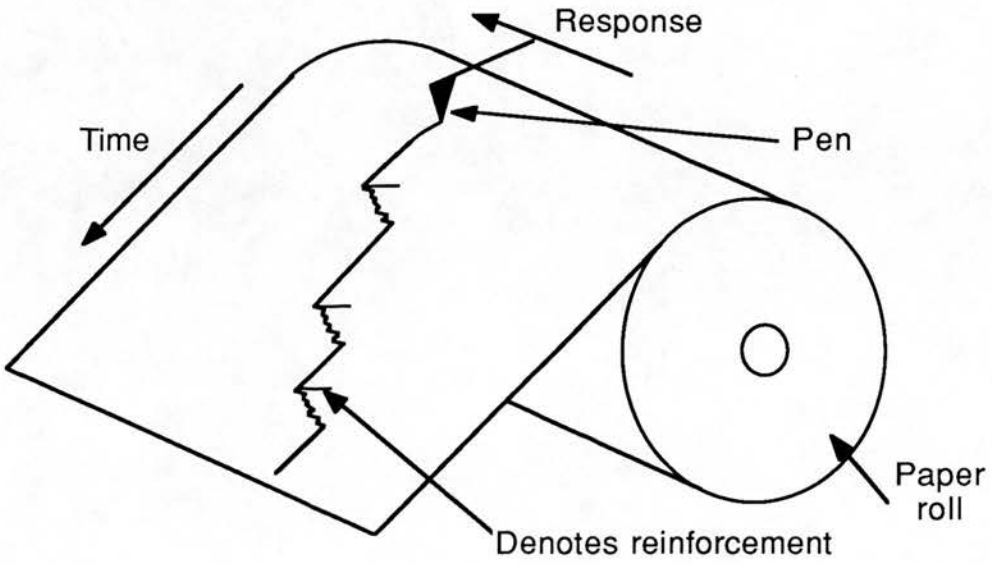


Figure 4.7. A cumulative recorder. (Adapted from Ferster and Skinner, 1957). In this example, the subject is responding on a fixed ratio 5 schedule of reinforcement.

However, the cumulative recorder was a relatively crude method of recording operant responses. Therefore, the computer controlled operant system stored the

operant responses digitally on a floppy disk. However, given that cumulative records allow a quick, visual check of the subject's response rate, software was written to plot cumulative records using the digital data. A number of such plots are used in Chapter 6 to show features which are relevant to the discussion.

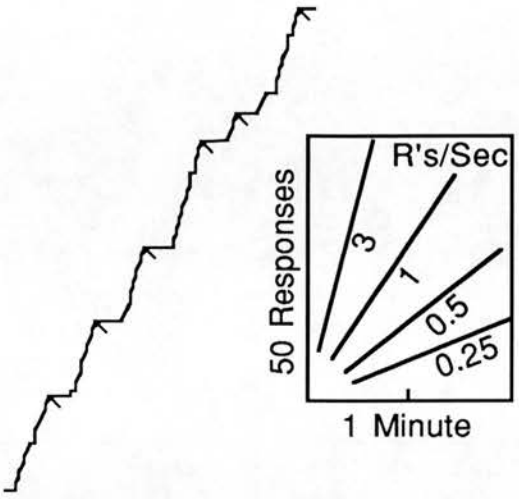
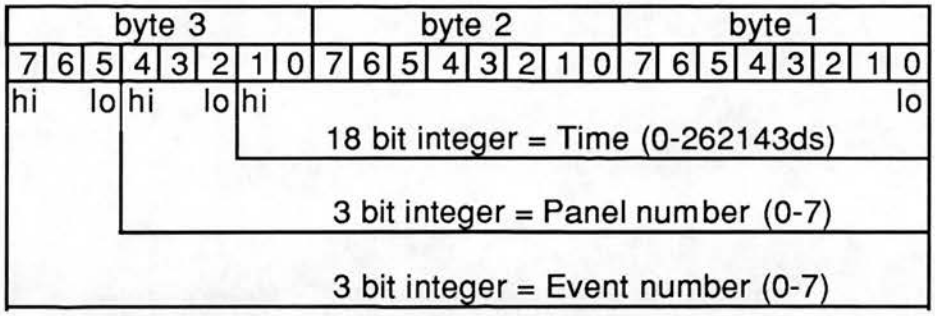


Figure 4.8. A typical cumulative record. The operant response rate can be estimated using the slopes shown in the rectangle.

To optimise storage space, the operant records were stored in a compact fixed length format. Each record was held in three bytes using the format shown in Figure 4.9. `PROCsave` recorded the current time, in deci-seconds, and the event code (which was passed to the routine as a parameter) in a temporary three byte `buffer`. This was then transferred to the end of the main buffer which was held in sideways RAM. The variable `pointer` was set to the address of next free space in the main buffer. `PROCfile` simply saved the entire data buffer as a single file on the current filing system.



Event numbers:
0 Good key peck i.e. when the key light is on
1 Bad key peck i.e. when the key light is out
2 Food reinforcement
3 Subject fed i.e. broke an infra-red beam across the doorway
4 CS on, or Fright discriminative stimulus (S^D) on
5 US delivered, or Fright
6 Food S^D on, or Food/Fright S^D off
7 Heart rate follows (1 byte)

Figure 4.9. The format of one data record.

4.5. Control software used for the experiments

The operant control program described in the previous section was extended to incorporate routines specific to the conditioned suppression and passive avoidance experiments. These extensions are outlined below.

4.5.1. Conditioned suppression experiment

The version of the operant software used for the conditioned suppression experiment had the following extensions:

- the ability to simultaneously control five panels
- routines to automatically teach the birds to perform the operant response (a process known as 'auto-shaping')
- a 'spreadsheet' type user interface which allowed the easy modification of the various experimental parameters in real time
- recording when the conditioned stimulus was switched on and off

All of these extensions were quite trivial, and were highly specific to the one experiment. Consequently, the listings for these routines are not given.

4.5.2. Passive avoidance experiment

The version of the operant software for the passive avoidance experiment had the following extensions:

• the ability to simultaneously control four panels

• to generate the tones used for the discriminative stimulus (S^D) and to control which panel received the S^D at any one time

• to record the type of S^D, and when it was switched on and off

• to record when the subject received a fright

• to record the heart rate

The majority of these extensions are quite trivial, and were highly specific to the one experiment. Consequently they do not warrant program listings. However, to ensure accurate processing of the signal from the heart rate transmitters, the routine to record the heart rate had to be written in 6502 assembly language. This routine, which may be of general use, is listed in Appendix II.

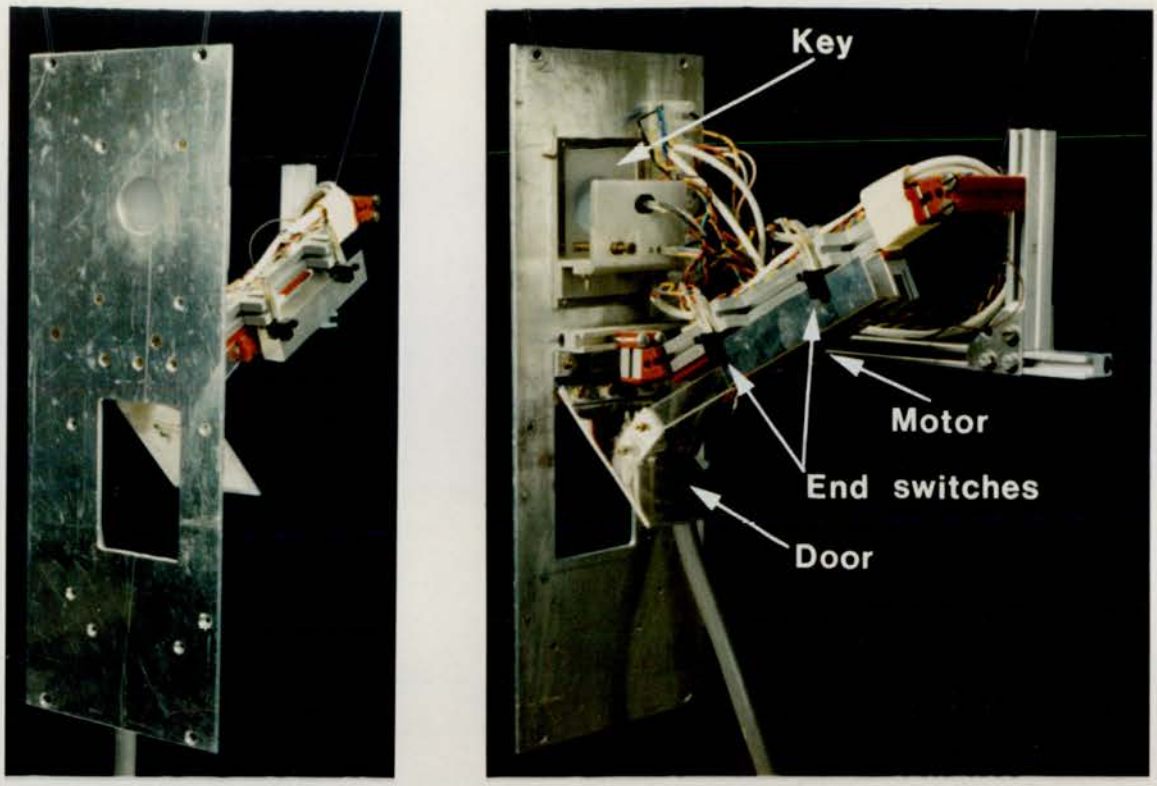


Plate Ia. The operant panel

Plate Ib. S-line (left) and T-line (right) hens

CHAPTER 5 Shuttle Avoidance

5.1. Introduction

The basic principle of avoidance conditioning was introduced in Chapter 2. Although any behaviour pattern could be chosen[1] as the avoidance response, locomotor activity (i.e. walking, running or flying away from the impending fright) has been the one most widely used. One of the main problems in early experiments using this type of conditioning was in returning the subject back to the location where it received exposure to the aversive stimulus. Once the animal had moved away from the impending fright, it invariably had to be picked up and placed back in the area where the fright was delivered. This extra handling between trials not only meant more work for the experimenter, but as the animal may have found handling itself aversive, may have confounded the experimental treatment.

This problem was overcome by using the 'Shuttle box' developed by Gentry (1934). This was simply a rectangular chamber fitted at either end with a light and buzzer, and with a mesh floor which could be electrified. The conditioning procedure consisted of switching on the light and buzzer for a short period, and then as they were switched off, electrifying the cage floor. This initially caused the experimental subject, usually a rat, to run about. As soon as the animal moved over the mid-line of the chamber, the shock was terminated. In subsequent trials, the procedure was initiated in whichever side of the box the rat happened to be at the time. The rat could, therefore, avoid further shocks by 'shuttling' to and fro between the two sides of the box whenever the light and buzzer were activated (hence the term shuttle avoidance). There was no such thing as a 'safe' side, as the subject could receive shocks in either side of the box. This allowed the procedure to be automated, even to the extent of using photocells to determine exactly where in

[1] However, as pointed out earlier, the fact that an experimenter chooses to reinforce a response does not necessarily mean that the animal is able to acquire the response as an avoidance response.

the box the animal was at any given time so that the appropriate area of floor could be electrified. (Unfortunately, this often resulted in many psychologists simply putting the subject in the box and then letting the equipment control the experiment whilst they got on with other things. If only they had stayed to watch the subject, they would have had a much better idea why the subject often failed to learn the required response.)

Given the relative convenience of the technique, shuttle avoidance has been widely used in the field of experimental psychology. Although the majority of studies have used electric shock as the aversive stimulus, other stimuli have been used. For example, rats can readily learn a shuttle avoidance task to avoid a blast of compressed air (Ray, 1966).

Shuttle avoidance has also been demonstrated in species other than the laboratory rat. Guinea pigs (Rabedeau and Webster, 1970), pigs (Karas, Willham and Cox, 1962; Baldwin and Stephens, 1973), cats (Lubar and Perachio, 1965; Krieckhaus and Chi, 1966), fish (Behrend and Bitterman, 1964) and pigeons (Macphail, 1968) have all been shown to learn shuttle avoidance tasks.

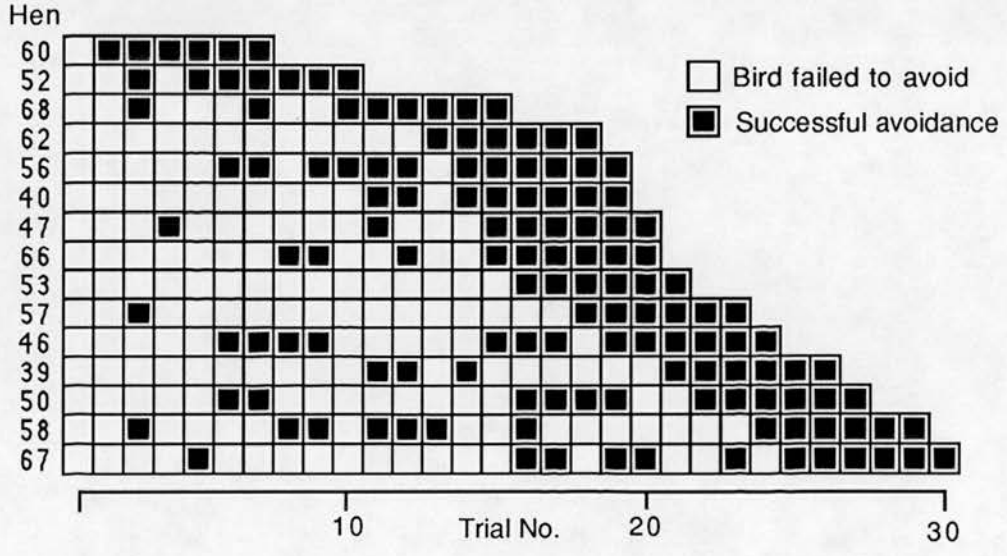


Figure 5.1. I.J.H.Duncan's (pers. comm.) avoidance results.

The technique has been demonstrated in the domestic fowl. Krieckhaus and Wagman (1967) showed that White Leghorn cockerels could learn to avoid an electric shock (2000V, 4-5mA) given a five second auditory warning stimulus. During the 11 days of testing, 11 out of the 15 birds tested reached the criterion of learning to avoid the electric shock on 17 out of 20 trials for three consecutive days. I.J.H.Duncan (pers. comm.) showed that Rhode Island Red x Light Sussex hybrid hens could learn to avoid a rapidly inflating balloon given a visual (panel light)

warning stimulus. I.J.H.Duncan's (pers. comm.) results are summarized in Figure 5.1. All the subjects tested reached the criterion of learning to avoid the balloon on six consecutive trials after less than 30 trials.

Unfortunately, the experiments performed by Krieckhaus and Wagman (1966) and I.J.H.Duncan (pers. comm.) did not use any control groups. It is, therefore, possible that the results they recorded were due to the birds simply escaping from the CS and not avoiding the impending shock or fright. Although the two studies used different strains (and sexes) of birds, no one study has investigated strain differences in shuttle avoidance in domestic fowl. Different strains of domestic fowl show different behavioural and physiological reactions to frightening stimuli (Duncan and Filshie, 1979), and it is possible that they may differ in their ability to acquire aversion learning tasks. The aim of this study was, therefore, to investigate shuttle avoidance in two different strains of laying hen in a properly controlled experiment.

5.2. Materials and methods

The subjects were tested in a 'shuttle box' (Figure 5.2). This consisted of a wooden box (0.90 m x 0.60 m x 0.60 m) which was divided into two equal sized compartments by a partition. A doorway (0.18 m x 0.45 m) in the partition allowed the birds free access to either compartment. Each compartment was fitted with an indicator lamp (the warning stimulus) and a balloon. The balloon could be rapidly inflated with compressed air, and this provided a potent but controlled aversive stimulus (Duncan and Filshie, 1979). Food and water were available *ad libitum* in both compartments. A muslin, one-way screen was positioned in front of the box so that the experimenter could control the apparatus without being seen by the subject.

For the experimental treatment, the warning light was switched on for ten seconds before the balloon was inflated. However, if the bird moved into the other compartment during the presentation of the light (the avoidance response), the balloon was not inflated. If the bird failed to avoid, the experimenter recorded whether or not the bird escaped from the balloon (i.e. whether or not it moved into the other compartment whilst the balloon was still inflated). As well as recording the avoidance and, if appropriate, the escape behaviour, general qualitative observations about the bird's behaviour during each trial were also noted.

It is possible that the birds found the warning stimulus itself aversive and were simply escaping from it rather than learning to avoid the balloon. A second group was, therefore, subjected to a control treatment. This involved presenting

the warning light and inflating the balloon at random i.e. with no explicit association between the two. This truly random control procedure was first proposed by Rescorla (1967), and is discussed further in Chapter 6.

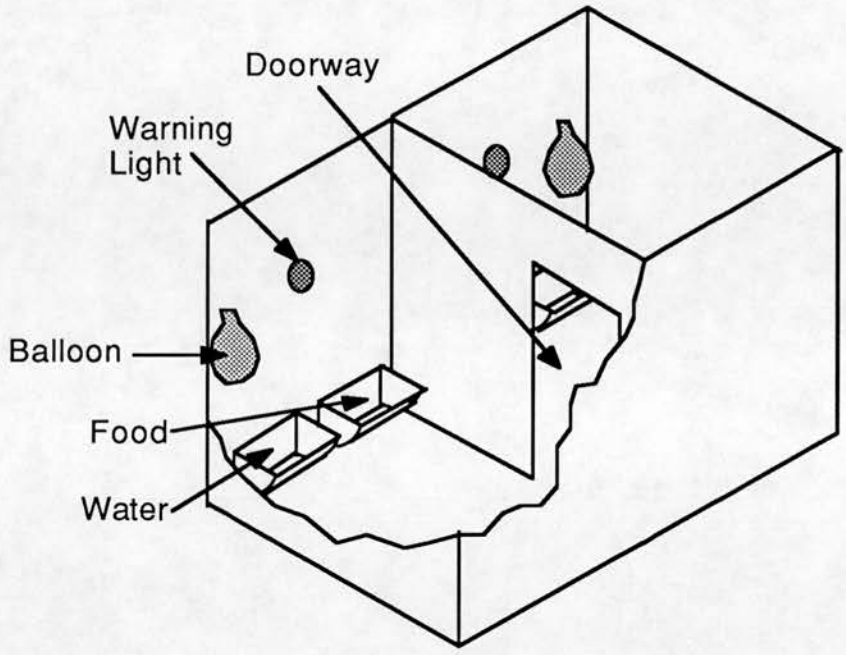


Figure 5.2. A cut-away view of the shuttle box.

To test the generality of the procedure, two strains of laying hens were used (Plate 1b). The first, known as T-line, was a medium body-weight Light Sussex x Rhode Island Red hybrid, and is usually described as 'placid'; the second, known as S-line, was a light body-weight White Leghorn hybrid, and is usually described as 'flighty' (Duncan and Filshie, 1979). Ten birds of each strain received the experimental treatment, and ten the random control treatment. This resulted in a 2 x 2 experimental design, with four groups; T-line experimental (TE), S-line experimental (SE), T-line random control (TC) and S-line random control (SC).

Each subject was tested in a single session until it reached a criterion of learning to avoid the balloon on five consecutive trials, or to a maximum of thirty trials. The inter-trial interval was randomly varied from six to twelve minutes. Twenty-four hours prior to testing, each bird was placed in a 'dummy' shuttle box, i.e. identical to the test box, except no balloons or lights were fitted. This allowed the birds to become accustomed to the new environment and the layout of the box.

5.3. Results

Figure 5.3 summarizes the results. Figure 5.4 shows the avoidance results. As the performance of birds which learnt the avoidance response was measured on a different scale to those which did not (i.e. number of trials to criterion as opposed to the proportion of avoidance trials) the data were not suitable for parametric analysis. However, the birds could be ranked according to their performance. Those birds which reached the criterion of learning were ranked according to the number of trials needed to reach the criterion. The remaining birds were then ranked below the 'avoiders', according to the proportion of trials on which they showed the avoidance response (Figure 5.3). These ranks were analysed using the Mann-Whitney non-parametric statistical test.

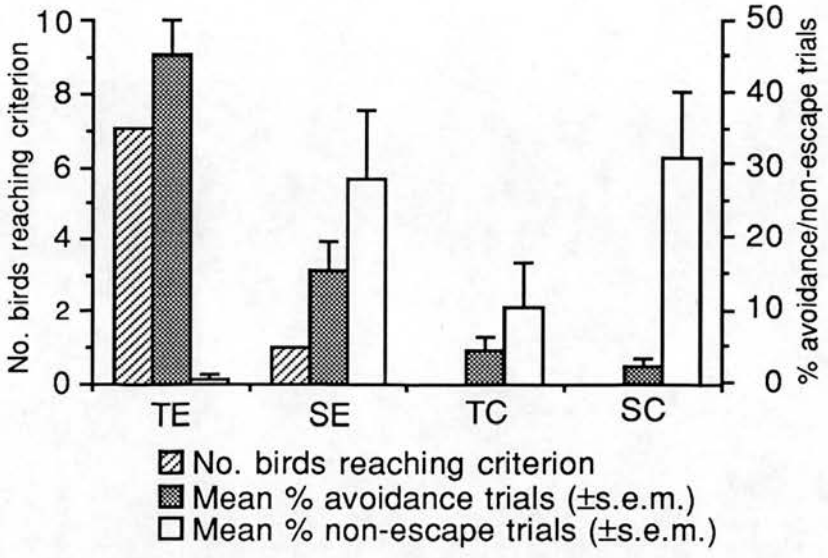


Figure 5.3. A summary of the results, showing the number of birds which reached the criterion of learning and the mean percentage of trials on which the birds showed avoidance or non-escape behaviour.

Of the forty birds tested, only eight reached the criterion of learning. Of these eight, seven were from the TE group and one from the SE group. Both the TE and SE groups showed more avoidance behaviour than their respective random controls ($U_{10,10} = 0$, $p < 0.002$; $U_{10,10} = 13.5$, $p < 0.01$), and the TE group showed more avoidance than the SE group ($U_{10,10} = 7$, $p < 0.01$). There was no significant difference between the TC and SC groups ($U_{10,10} = 40$, $p > 0.1$). There was no significant strain-treatment interaction ($U_{20,20} = 153.5$, $p > 0.1$). (Results from the TC and SE groups were added together and compared with the sum of the TE and SC results in order to test for an interaction.)

The escape behaviour results are summarized in Figure 5.5. As with the avoidance results, the birds have been ranked according to the proportion of trials in which they escaped. The TE group showed more escape behaviour than the SE group ($U_{10,10} = 8.5, p < 0.002$), and the TC group showed more than the SC group ($U_{10,10} = 22.5, p < 0.05$). There were no significant differences between the TE or SE groups and their respective random controls ($U_{10,10} = 34, p > 0.1$; $U_{10,10} = 49$, $p > 0.10$), and there was not a significant strain-treatment interaction ($U_{20,20} = 171, p > 0.10$).

Note that the technique used for testing for an interaction between the main variables is described further in Meddis (1984). Just as the main effects can be studied by combining groups with one common element i.e. strain by looking at (TE + TC) vs (SE + SC) and treatment by looking at (TE + SE) and (TC + SC), the interaction can be studied by combining groups with mutually exclusive elements i.e. (TE + SC) vs (TC + SE).

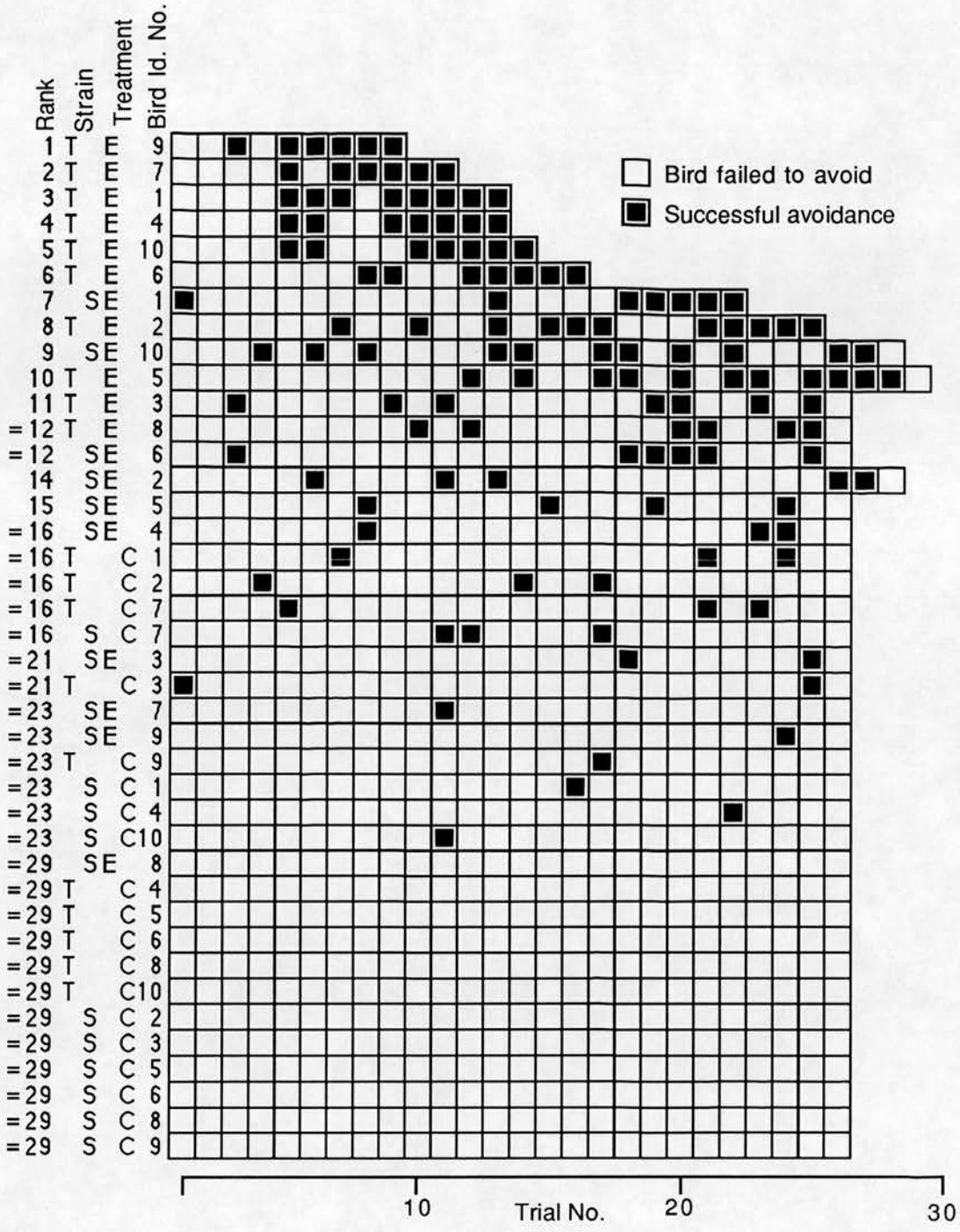


Figure 5.4. The avoidance results. Each box represents one trial. The rank order, bird strain, treatment and identification number is given on the left-hand side of the figure. Note that the ranks shown in the first column were derived using a 'common' ranking procedure i.e. tied values were all given the lowest numerical rank. The ranks used in the calculation of the test statistics were derived using a 'statistical' ranking procedure i.e. tied values were all given the mean rank of the tied values.

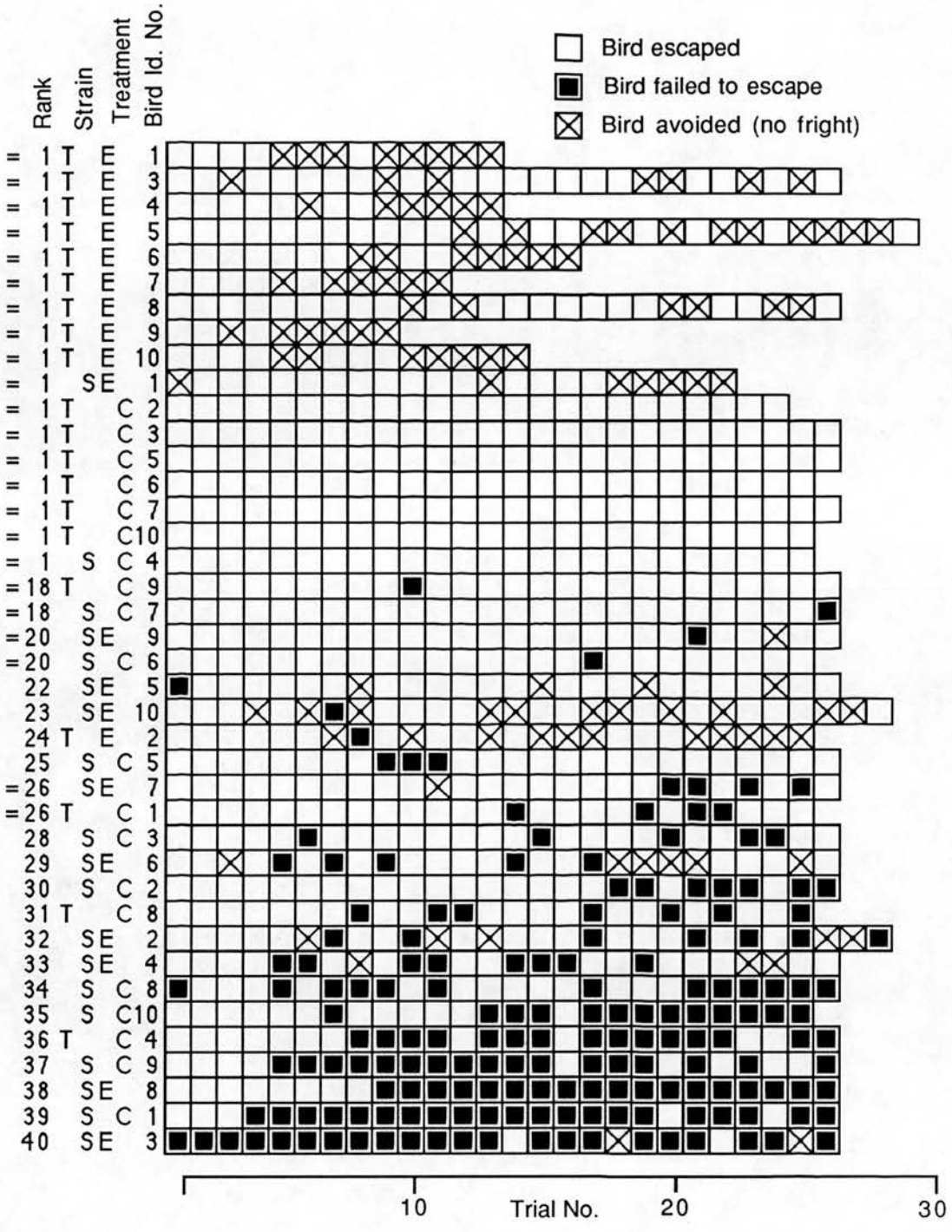


Figure 5.5. The escape behaviour results.

5.4. Discussion

The T-line experimental group generally learnt to avoid being frightened[1]. Although the S-line experimental group showed significantly more avoidance behaviour than the S-line random controls, they showed significantly less than the T-line experimental birds, with only one of the ten SE birds reaching the criterion of learning. Why did this happen? A number of possible explanations are discussed below.

5.4.1. Failure to learn the light→ balloon association

According to two-factor theory (discussed in Chapter 2), an avoidance task requires the subjects to learn two distinct associations. They first have to learn that the warning stimulus precedes the aversive stimulus. This is the classically conditioned stage, with the light acting as a CS predicting the aversive US. Having learnt this association, the subjects then have to learn that by performing a particular response they can avoid being frightened. This is the instrumental stage, which, according to two-factor theory, is reinforced by the termination of the CS. Clearly, this second stage can only occur if the subjects have first learnt the classically conditioned association. One possible explanation for the failure of some birds to acquire the shuttle avoidance response in this experiment is that these birds failed to learn the classically conditioned association between the light and the balloon.

Chapter 6 describes an experiment which, amongst other things, was designed to investigate if these birds had learnt the light → balloon association. To summarize briefly the results from that experiment, the few birds which failed to learn the avoidance response did show a suppression of operant responding when the warning light was switched on. This suggests that these birds had learnt the light→balloon association. Although there were some reservations about this conclusion (discussed in Chapter 6), the hypothesis that the failure of some birds to learn the avoidance response was due to them failing to learn the light→balloon association can probably be rejected. Consequently, the failure of some birds to learn the shuttle avoidance task was probably due to them failing to learn that by moving into the adjacent compartment they could avoid the impending fright. The

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[1] Note that there was no significant difference ($U_{10,15} = 124.5$, $p > 0.10$) in the number of trials to criterion of learning between the T-line experimental subjects tested in this experiment and the birds tested by I.J.H.Duncan (pers.comm.).

following sections discuss a number of possible explanations of why some birds failed to acquire the actual response required to avoid the balloon.

5.4.2. Strain-specific defence reactions

The description of S-lines being 'flighty' and T-lines 'placid' (Duncan and Filshie, 1979) was certainly borne out by the behavioural responses recorded during testing. The S-line birds initially showed exaggerated escape activity when frightened, often attempting to fly out of the box. Such frantic behaviour did not usually result in the bird getting through the doorway, even though they still appeared to be trying to escape from the balloon[1]. During the later trials, many of the S-lines suddenly started to freeze when frightened, often becoming completely motionless for the remainder of the experiment. The T-lines, however, generally showed restrained escape activity, often simply walking into the other compartment when frightened. None of the T-line experimental birds ever froze, and only two T-line random controls showed freezing behaviour. It is therefore possible that the two strains possess different, strain-specific defence reactions; the S-lines either freeze or attempt to fly away from potential danger whereas the T-lines are quite willing to walk away from such a situation.

This idea of strain-specific defence reactions is similar to Bolles' (1970) notion of species-specific defence reactions (SSDRs), introduced in Chapter 2 of this thesis. Bolles proposed that for an avoidance response to be readily learnt it should be one of the animal's natural defence reactions. It is, therefore, possible that the response required in the shuttle avoidance task i.e. walking through a door-way, whilst being compatible with the T-lines defence reaction, was not compatible with the 'flight' or 'freeze' responses shown by the S-lines.

This appears a highly plausible explanation for the failure of an animal to learn an avoidance task. However, as Mackintosh (1983) points out:

> "...there is an obvious danger of circularity to this [Bolles'] line of reasoning. Is an avoidance response learned readily? It must form part of that animal's species-specific defence repertoire, i.e. be a classical CR. How do we know it is? Because it is learnt readily as an avoidance response. The analysis needs some independent supporting evidence, in the form of either ethological observation of the defensive behaviour of animals under natural conditions, or of direct measures of the CRs elicited by a classical contingency in the experimental situation. There is little or none of the former and not much more of the latter."

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[1] These trials were recorded as non-escape trials (even though the bird was showing escape behaviour) because the bird did not actually escape from the balloon i.e. it did not move into the adjacent compartment.

With this comment in mind, a pilot study was performed to investigate the natural defence reactions of the two strains of hens.

Before describing this study, it is important to emphasize that it was very much a pilot study and no quantitative data were recorded. Although this meant that no statistical analysis was possible, the results were very clear cut. However, the findings must be considered to be tentative until verified by a larger scale experiment. Consequently, the study does not warrant a chapter to itself, and is therefore described below.

The subjects were six S-line and six T-line sexually mature laying hens. They were tested individually in an open room (7.65m x 4.60m x 2.45m), a plan of which is shown in Figure 5.6. Four dishes, two containing food and two water, were placed in a square in the centre of the floor. A balloon, which could be remotely inflated, was mounted in the centre of the four dishes (Figure 5.7). There were three experimental treatments. The first gave the subject complete freedom to escape, i.e. there was no partition surrounding the central dishes. Under treatments two and three, the central dishes were surrounded by a low partition (1.10m square, 0.48m high) which had either four or two doors (0.24m x 0.30m) respectively (Figure 5.6). Under treatments two and three, the bird could either escape from the balloon by running through one of the door-ways, or by jumping or flying over the partition. Two closed circuit television cameras, one at either end of the room, allowed the experimenter to observe the birds remotely.

The results were surprising. Over the total of approximately sixty experimental trials, no subject, regardless of strain, ever attempted to fly away from the balloon, even when confined in close proximity to it, and no subject ever froze. All subjects, regardless of strain, ran away from the balloon. Under this experimental situation then, the S-line birds showed exactly the same defensive reactions as the T-line birds. Why should the S-line birds show either a 'flight' or 'freeze' response in a shuttle box but run away in an open room?

Perhaps the most plausible explanation is in the relative 'effectiveness' of the escape response in the open room compared to the shuttle box. In the shuttle avoidance experiment, the birds could only escape into the other compartment. This was not a very effective escape response as it did not place much distance between the subject and the aversive stimulus. However, in the defence reaction experiment, the birds could escape to a place much further away from the aversive stimulus. Indeed, this was invariably the case, with the majority of birds of both strains running to one of the walls. This situation is similar to that found in nature,

where an animal is usually free to put as much distance between itself and, say, a predator, as it wishes.

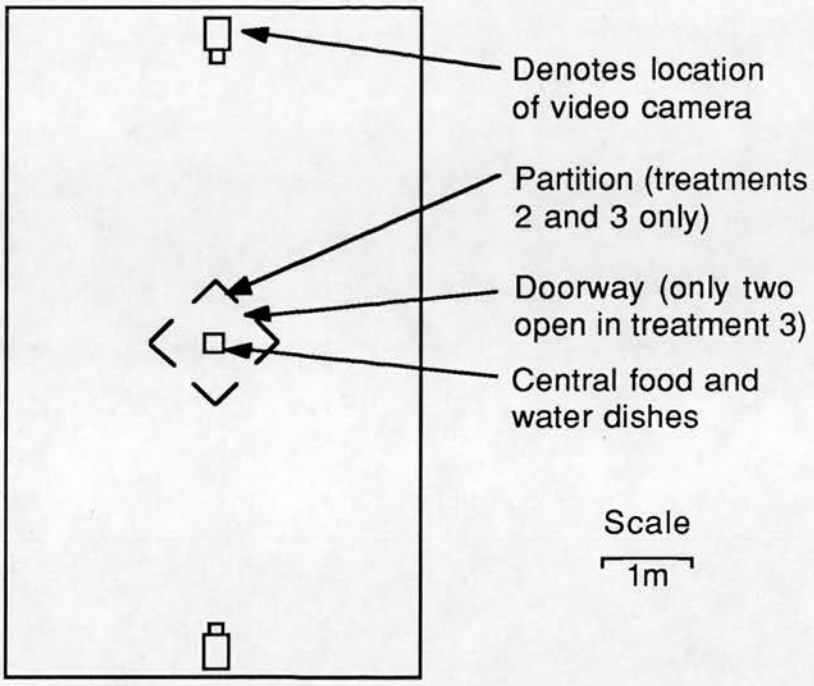

Figure 5.6. Plan view of the experimental room.

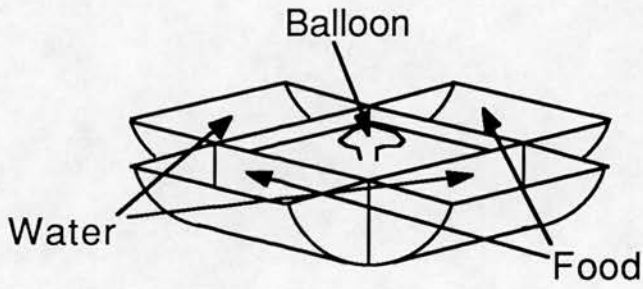

Figure 5.7. Food and water dishes and their relationship to the balloon.

This experiment demonstrated that running *is* one of the S-line's natural defence reactions and so, according to Bolles, it should be learnt as an avoidance response. Did Bolles get it wrong?

Although the main proposal put forward by Bolles (1970) was "that *an* R_a [avoidance response] *can be rapidly acquired only if it is an SSDR*", and that "*an* R_a *is rapidly acquired only by the suppression of other SSDRs*" (p.34, italics in original), he does acknowledge that the effectiveness of the response has an important role to play :

"... running will not be acquired as an R_a, at least not very readily, unless the running response is effective for flight, that is, effective in the functional sense that it takes the rat out of the situation." (p.35).

However, certain species can acquire a running response in a shuttle box. For example, Solomon and Wynne (1953) demonstrated that dogs can rapidly acquire a shuttle avoidance response. Bolles' explanation of this finding was that the dog, unlike the rat, does not usually attempt to flee completely from an aversive situation, but "stands off at some distance". Consequently the dog sees a shuttle avoidance response as effectively placing the required distance between itself and the aversive stimulus, whereas the rat, which wants to escape completely, does not.

The results of the defence reaction pilot study suggest that Bolles was generally right, it is just that his emphasis was wrong. Bolles' principal proposal was that for an avoidance response to be readily learnt, it must form part of the animal's defence response repertoire. He then admits that if the SSDR is not an effective escape response then it may not be learnt. A far more logical conclusion is that an avoidance response is rapidly acquired only if *the animal perceives the response as being effective*. The response need *not* be an SSDR. However, the innate defence reactions have no doubt evolved because they are effective escape/avoidance responses, at least in the wild. It is probable that an animal in a potentially threatening situation would, at least initially, resort to these defence reactions, simply because they generally are effective. Therefore, although there are examples of effective avoidance responses being readily acquired (e.g. Maatsch [1959] showed that a rat which receives an electric shock in a box can learn to avoid the shock by jumping out of the box in just one trial), these examples also support Bolles' theory because such avoidance responses are also SSDRs.

However, the idea that it is the efficiency of a response which makes it acquirable as an avoidance response rather than it being an SSDR is supported by the findings of an experiment by Davis, Babbini and Huneycutt (1967). The experiment is described in some detail in Chapter 7, but it essentially compared a shuttle avoidance response with a one-way avoidance response in the same apparatus. Both the one-way and shuttle avoidance tasks required the animal to walk through a doorway i.e. they shared a common SSDR response. Consequently, according to Bolles, the two responses should have been equally as easy (or difficult) to learn as they shared the same topography. However, subjects required to perform the one-way response showed significantly more avoidance than the shuttle subjects. This suggests that there is something over and above the

topography of the response which results in the one-way response being acquired more readily than the shuttle response. This could be the perceived efficiency of the one-way response, which makes it a more attractive an avoidance response than a shuttle response and consequently a one-way task is easier to learn.

This is supported by the fact that in the shuttle avoidance experiment, TE9, which reached the criterion of learning after only nine trials, was effectively performing a one-way response. The bird always received exposure to the warning stimulus and any subsequent fright in the left-hand chamber. The bird would escape/avoid into the right-hand chamber, but then always moved back into the left-hand chamber before the start of the next trial. Although it is very difficult to explain why the bird should have done this, it is possible that it resulted in the bird perceiving the right-hand compartment as being 'safe', and that moving into it was therefore an effective avoidance response. When this bird was subsequently tested in the conditioned suppression experiment (described in Chapter 6), the bird avoided the balloon on the first trial by moving from the left to the right compartment. However, the bird stayed in the right-hand compartment and failed to avoid the fright on the next trial. During the subsequent ten trials, the bird would panic when the warning light came on, running to and fro between the two compartments, avoiding the balloon on only five trials. It was almost as if the bird had become 'confused' by an 'unexpected' fright in the right hand chamber, which again supports the idea that this bird initially perceived the right-hand compartment as being 'safe'.

It is, therefore, possible that it was the shuttle nature of the avoidance response which resulted in the poor performance in some birds. The fact that the subjects received frights in both sides of the shuttle box meant that there was no one place which was always 'safe'. This possibility was investigated by the experiment described in Chapter 7.

The problem with this interpretation of the shuttle avoidance results is that the freezing response shown by the S-line birds was *not* an effective escape response. The birds which froze continued to receive exposure to the aversive stimulus. Why then did freezing persist? The following two sub-sections propose two different explanations to account for this problem.

5.4.3. Freezing as an instrumental avoidance response

Bolles (1970) suggested, albeit indirectly, that freezing (and other SSDRs) were examples of classical CRs. He first recalled a fable which had often been used to show how the study of avoidance learning in the laboratory could be used

to "explain" how animals survive in the wild. Bolles' slightly mocking account of the fable went like this:

> "Once upon a time there was a little animal who ran around in the forest. One day while he was running around, our hero was suddenly attacked by a predator. He was hurt and, of course, frightened, but he was lucky and managed to escape from the predator. He was able to get away and safely back to his home. The fable continues: Some time later our furry friend was again running around the forest, which was his custom, when suddenly he perceived a conditioned stimulus. He heard or saw or smelled some stimulus which on the earlier occasion had preceded the attack by the predator. Now on this occasion our friend became frightened, he immediately took flight as he had on the previous occasion, and quickly got safely back home. So this time our hero managed to avoid attack (and possibly worse) by responding appropriately to a cue which signalled danger; he did not have to weather another attack. And from that day hence the little animal who ran around in the forest continued to avoid the predator because the precariousness of his situation prevented, somehow, his becoming careless or forgetful." (p.32)

Bolles proposed that such a tale was "utter nonsense". He went on:

> "The parameters of the situation make it impossible for there to be any learning. Thus, no real-life predator is going to present cues just before it attacks...What keeps our little friends alive in the forest has nothing to do with avoidance learning as we ordinarily conceive of it or investigate it in the laboratory...What keeps animals alive in the wild is that they have very effective *innate* defensive reactions which occur when they encounter any kind of new or sudden stimulus" (p32-33, italics in original).

Although not explicitly stated, Bolles' use of the phrase "innate defensive reactions" suggests that he saw the avoidance response as a simple CR i.e. an example of classical conditioning. This idea has been supported by subsequent studies in which freezing has been shown to be influenced by variables associated with classical conditioning. For example Davitz, Mason, Mowrer and Viek (1957) found that the CS-US interval can influence the degree of freezing. Freezing has been shown to occur more readily with CSs than with novel control stimuli (Blanchard and Blanchard, 1969; Bouton and Bolles, 1979). Sigmundi and Bolles (1983) found that an auditory CS evokes more freezing in rats than a visual CS. Such findings lead Bouton and Bolles (1980) to conclude that "freezing appears to be a respondent, in that it is controlled by its antecedents rather than its consequences".

Whilst I would generally support the conclusion of Bouton and Bolles (1980) with regards to freezing in response to electric shock, it is possible that electric

shock induced freezing has a different basis to the freezing produced in response to a looming stimulus (such as the inflating balloon).

In nature, freezing occurs in response to two different situations (Gallup and Maser, 1977). Firstly, if the prey animal is suitably camouflaged, it may be able to avoid detection by a hunting predator by staying motionless i.e. freezing. The simple fact that the prey animal stays still means that the visual system of the predator finds it harder to detect. If this fails and the predator does see and attack the prey, the prey animal would probably attempt to flee. If it were caught, it would initially struggle to escape. If escape were impossible, the animal may be able to escape by feigning death, that is by freezing. This may fool the predator into thinking that the prey is dead, and it may release its grip, giving the prey the opportunity to escape.

The freezing response produced by electric shock is probably of the 'death feigning' variety. The animal may perceive electric shock as being caught by a predator, the pain the shock produces being equivalent to that which may be produced when grasped by the jaws or talons of a predator. Under natural conditions, animals are not going to have much opportunity to learn the benefits of such a response, and consequently it is almost certainly innate. In contrast, the freezing which occurred in response to the inflating balloon was probably of the 'stay still to avoid detection' type. Whilst this response may also be innate, there would be a greater opportunity for an animal to learn the benefits of such a response in the wild. Whilst the probability of an animal being caught and then escaping are probably very low, avoiding capture by a predator by freezing probably occurs quite regularly in certain species.

The hens may have perceived the balloon as a predator which occasionally appeared in the shuttle box. Any freezing behaviour shown by some hens could have been reinforced by the fact that the 'predator' did not actually make contact with the birds and that it quickly 'went away' again. The birds could, therefore, have superstitiously associated the freezing response with the 'predator going away' and, consequently, the freezing response could have been an instrumentally reinforced avoidance response. From the experimenter's point of view it does not appear to be a very efficient avoidance response as the animal is *not* actually avoiding the aversive stimulus. However, the animal is not to 'know' this, and it may have perceived that if it tried to escape the predator would have caught it. In this respect the birds may have seen freezing as an effective avoidance response, as they were avoiding being killed.

5.4.4. Learned helplessness

It is apparent from Figure 5.3 that many of the S-line birds were often not even escaping from the balloon. As was described in the previous section, these birds initially showed frantic escape behaviour. During later trials, these birds started to freeze, and a number of subjects entered a catatonic state which lasted for the remainder of the experiment. This may be similar to the phenomenon of learned helplessness, which was first reported in dogs (Seligman and Maier, 1967), but has subsequently been reported to occur in rats (Hannum, Rosellini and Seligman, 1976), mice (Braud, Wepmann and Russo, 1969), cats (Seward and Humphrey, 1967), goldfish (Padilla, Padilla, Ketterer and Giacalone, 1970), man (Danker-Brown and Baucom, 1982), pigeons (Welker, 1976) and chickens (Job, 1987). It is believed that the learned helplessness effect is due to the subject learning that the termination of the aversive stimulus is unrelated to their responding (Maier and Seligman, 1976; Alloy and Seligman, 1979). Faced with inescapable shock, the subjects essentially 'give up', becoming 'helpless'.

The hypothesis that learned helplessness was the reason many subjects failed to learn the avoidance response in this experiment faces one major difficulty. The birds *could* escape from the balloon (by running into the other compartment) and so were not exposed to an inescapable aversive stimulus, the principal condition required for learned helplessness. It is, however, possible that the birds had been exposed to inescapable frights before the start of the experiment. All the subjects were reared in single battery cages in one of the Research Station's poultry houses. Under these conditions the birds were exposed to a number of different husbandry procedures, including cage dusting. This involved the cage being dusted with a large, soft-bristled brush. As we shall see in Chapters 7 and 8, domestic fowl find this treatment very aversive. Given the relatively small size of a battery cage, the birds were unable to escape from this stimulus. Consequently, the weekly cage dusting may have acted as an inescapable aversive stimulus which could have led to the development of learned helplessness in a number of the birds. However, only one subject, SE3, showed the effect from the first experimental trial. All of the other subjects which showed freezing initially showed escape behaviour. It is, therefore, unlikely that the effect was established prior to experimental testing. (This could be tested by rearing two groups of birds, one with and one without cage dusting, and then comparing the relative ability of birds from the two groups to learn a shuttle avoidance response.)

A more feasible explanation for the possible development of learned helplessness concerns the birds' concept of an escape response. Although, from

the experimenter's point of view, the birds could actually escape from the balloon by running through the doorway, it is possible that they did not 'see' this as an effective escape response. Indeed, this seems quite likely given the fact that the bird received yet another trial a few minutes later. This is supported by the fact that some birds attempted to fly out of the box, sometimes even after they had moved into the other compartment. These birds appeared to want to completely escape from the shuttle box. The fact that they could not resulted in the birds being exposed to what *they* perceived as an inescapable fright. Consequently, the requisite conditions for learned helplessness may have existed in the experiment after all.

5.6. Conclusion

The principal conclusion from the shuttle avoidance experiment is that shuttle avoidance is *not* a suitable measure of aversion for the assessment of the welfare of domestic hens. This is because the response was learnt by only half the subjects tested, the majority of which were of one strain, and consequently fails to meet the first criterion proposed in Chapter 3. It is believed that the task was not readily learnt by some birds (particularly the S-lines) because the required shuttle avoidance response was incompatible with the frantic escape attempts followed by freezing shown by these birds.

CHAPTER 6 Conditioned Suppression

6.1. Introduction

The phenomenon of conditioned suppression[1] was first observed by Estes and Skinner (1941). They noticed that pigeons showed a suppression in operant responding after the onset of CS which had previously been paired with an electric shock (the US). They attributed this response suppression to a state of anxiety which was caused by the CS. Since this initial demonstration, the phenomenon has been investigated under a wide range of experimental situations, and the technique has become "the *de rigeur* method of measuring aversive conditioning" (Bouton and Bolles, 1980). Several thorough reviews are available (Davis, 1968; Lyon, 1968; Blackman, 1977; Davis and Wright, 1979).

The phenomenon has been found to occur with rats (Kamin and Schaub, 1963), guinea pigs (Valenstein, 1959), cats (Brady and Conrad, 1960), dogs (Waller and Waller, 1963), Rhesus monkeys (Goldberg and Schuster, 1967) and goldfish (Geller, 1964). Conditioned suppression has also been demonstrated in some domestic animals, including sheep (Liddell, James and Anderson, 1935; Leach, Warrington and Wotton, 1980) and pigs (Baldwin and Stephens, 1973; Dantzer and Baldwin, 1974; Dantzer and Mormède, 1980).

A range of stimuli other than the 'traditional' lights or tones had been found to act as CSs. Morris (1966) found that a 15 second exposure to X-rays could

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[1] The term conditioned emotional response (CER) has often been used interchangeably with the term conditioned suppression. However, as Davis (1968) points out, the two terms refer to different (but related) phenomena. Conditioned suppression studies record the suppression in operant response rate at the onset of a CS which has been paired with an aversive US. In contrast, the CER is a conditioned behavioural complex which occurs in the presence of a CS and which underlies the phenomenon of conditioned suppression. A CER experiment would, therefore, involve the direct measurement of classically conditioned autonomic behaviour e.g. heart rate or galvanic skin response.

establish conditioned suppression when associated with electric shock. The pain reactions of conspecifics has been shown to act as a CS in both rats (Church, 1959) and pigeons (Watanabe and Ono, 1986). Electrical stimulation of the visual cortex in peripherally blind rats can suppress bar pressing when associated with electric shock (Mogenson, 1962). The degree of suppression has been shown to be a positive monotonic function of the intensity of a noise CS (Kamin and Schaub, 1963). Pre-exposure to the CS (i.e. exposure to the CS before it is paired with the US) can retard the acquisition of conditioned suppression, and can result in 'inhibition of delay' i.e. less suppression at the beginning of a trial than at the end (Schachtman, Channell and Hall, 1987).

Although the majority of studies have used electric shock as the aversive US, a few other USs have been found to elicit response suppression. A loud tone (110 db) or a loud noise (114-120 db) have been shown to function as a US in establishing conditioned suppression in pigeons (Leitenberg, 1966). Nalorphine has been shown to produce conditioned suppression in morphine-dependent monkeys (Goldberg and Schuster, 1967). The acquisition and resistance to extinction of conditioned suppression are positively related to the intensity of an electric shock US (Annau and Kamin, 1961; Hendry and Van Toller, 1965; Millenson and Hendry, 1967).

Conditioned suppression has been used to monitor the levels of fear during the course of avoidance conditioning, and this could be potentially useful in determining why some subjects failed to learn the shuttle avoidance task described in Chapter 5. Kamin, Brimer and Black (1963) trained a number of groups of subjects to various criteria of acquisition and extinction of a shuttle-box avoidance response. They then measured the suppression of a food reinforced operant response in a Skinner box when the CS was presented. However, such 'off-line' testing (i.e. measuring the effect of the CS in a different piece of apparatus to the one in which the CS→US association was learnt) may result in some problems. The degree of suppression may be less that expected because the CS is presented out of context i.e. the subject may not associate the CS presentation in the Skinner box with the presentation of the US in the shuttle box. Alternatively, the subject may find the situation more aversive as it cannot perform the shuttle avoidance in the Skinner box.

A number of different operant schedules of reinforcement have been used, although the commonest has been variable interval (Davis and Wright, 1979).

The aim of the study reported in this chapter was two-fold. The principal aim was to investigate the phenomenon of conditioned suppression in the domestic

fowl. Secondly, it was hoped to use the technique to determine whether or not the subjects which failed to acquire the shuttle avoidance response had learnt the association between the warning stimulus and the balloon. This would be achieved using an 'on-line' approach i.e. measuring the suppression of operant responding in the shuttle box itself.

6.2. A critique of the analysis of response suppression

Two variables are recorded during a conditioned suppression experiment; response rate before CS onset i.e. the baseline rate (*b*), and response rate during CS presentation (*d*). The experimenter is interested in the effect of the CS on operant behaviour, which is shown by any difference between these two variables. Consequently, it is only natural to combine these two variables into one measure of this difference. The simplest way of doing this is to calculate the arithmetic difference, *b-d*. However, this only gives the absolute difference, which does not accurately reflect the degree of response suppression. For example, a subject performing 100 responses before and 90 responses during the CS will have the same value as a subject performing 10 before and none during, i.e. 10. However, it is intuitive to consider the second subject, who showed total response suppression after the onset of the CS, as having shown 'more' suppression than the first subject, and the measure should reflect this.

What is needed is a measure of the relative difference. This implies the use of some form of ratio. Hurwitz and Davis (1983) argued that any ratio measure of conditioned suppression was invalid, as the experimental treatment also resulted in changes in the baseline rate; i.e. a plot of baseline rate against trial number is usually U shaped. It is true that a ratio does not accurately reflect relative changes in two variables when a regression line fitted between the two has a non-zero intercept. However, a ratio is a perfectly acceptable measure of relative difference as long as the regression line intercepts an axis at (or at least very close to) the origin.

Traditionally, psychologists have used the suppression ratio, i.e. $d/(d+b)$ where *b* is the response rate prior to CS onset and *d* is the response rate during the CS[1]. Church (1969) discussed several alternatives to the suppression ratio. He estimated the strength of the relationship between various punishment conditions (e.g. intensity, duration, schedule, inter-trial interval) and the proposed

[1] In practice, *d* is the number of responses during the period when the CS is on, and *b* is the number of responses in the period of the same duration immediately prior to CS onset.

measure of suppression, using data collated from a number of studies. His results are summarized in Table 6.1.

Measure	Variance accounted for
d	46%
b-d	40%
d/b	53%
$\sqrt{d/b}$	54%
d/(d+b)	55%
θ (where tanθ=d/b)	55%

Table 6.1. The strength of the relationship between punishment conditions and a number of different measures of response suppression. b is the response rate before CS onset; d during the CS (from Church, 1969).

The simple measures of *d* and *b-d* accounted for significantly less of the variance than any of the ratio measures. There was, however, little to choose between the four variations of the ratio measure.

However, the suppression ratio (i.e. $d/[d+b]$) itself tends to distort the relative difference. For example, suppose a subject shows a 50% decrease in response rate after CS onset. It would seem logical that the measure should also show a 50% decrease. However, a response rate decrease of 50% results in a suppression ratio of 0.333. This is a decrease of only 33.3% compared with the ratio value when there is no change in response rate i.e. 0.5. Figure 6.1 shows the relationship between percentage reduction in response rate and various measures of response suppression. The non-linear relationship between the suppression ratio and the degree of suppression results in lower response rates having a proportionately greater effect. However, the use of the simple ratio of d/b gives, by definition, a linear relationship between the degree of suppression and the measure of suppression. Indeed, the suppression ratio could be considered as a transformation of the d/b ratio, similar to the tan θ or square root transformations. It is possible that some other transformation would yield a measure which accounted for even more of the variance than the suppression ratio or the tan θ transformation. Therefore, such a transformation should be used in preference to the suppression ratio if it gave better discrimination between the main effects of the experiment.

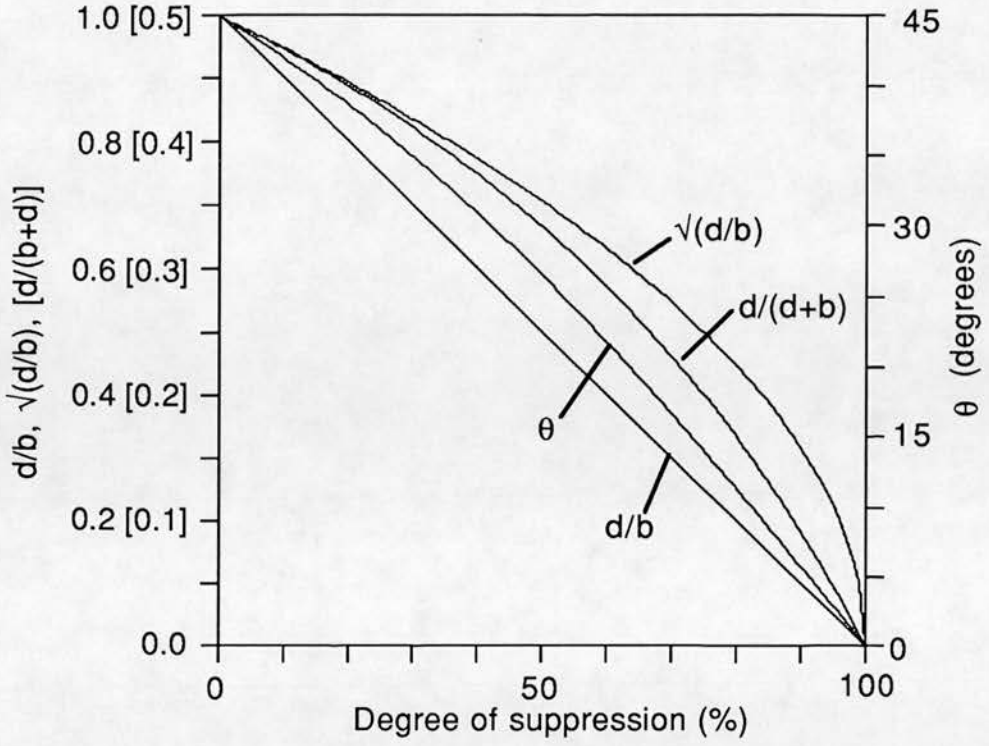

Figure 6.1. The relationship between the degree of suppression and a number of measures of suppression.

Why then has use of the suppression ratio persisted? The ratio $d/(d+b)$ does have one advantage over d/b. When b is zero but d is non-zero, $d/(d+b)$ has a value of 1.0, whereas d/b is infinite (and, therefore, undefined). However, in an ideal conditioned suppression experiment, b should always be greater than zero, i.e. there should be some baseline responding. A baseline response rate of zero tells us nothing about the suppressive effects of the CS. Therefore, the use of $d/(d+b)$ should confer no advantage over d/b in a well designed conditioned suppression experiment.

Church (1969) argued that the suppression ratio should continue to be used, because :

> "A new measure, however, should not replace an old one unless it is demonstrably superior. The traditional measure yields data that are comparable to the existing information and such comparability should not be sacrificed without compensation. Furthermore, because of its familiarity, the implications of a traditional measure are generally easier to comprehend than those of a new measure." (p117-118)

However, the traditional suppression ratio analysis of response suppression has used techniques which violated two basic principles of statistical analysis.

Firstly, it was traditional to give the ratio the value of 0.0 when both *d* and *b* were zero. However, the fact that the subject fails to respond at all either prior to or during the CS tells us nothing about the subject's reaction to the CS. Consequently, such trials must be regarded as 'missing values' and excluded from the analysis. Once suppression ratios had been calculated, they were traditionally analysed using an Analysis of Variance (ANOVA). However, as Church (1969) pointed out, there is usually a correlation between the mean and the variance of the suppression ratio for different treatments. As one of the criteria for an ANOVA is that variances should be homogeneous, it is wrong to use the technique without first ensuring that the data do not violate this assumption.

Given that the majority of studies reported in the aversion learning literature do not give adequate details of the method of analysis, the majority of these studies must be treated as suspect. Consequently, comparison with the results of previous studies cannot be used as an argument in favour of the suppression ratio. Given that the simple ratio reflects the degree of suppression more accurately than the suppression ratio, it is sensible to use the former in preference to the latter.

To summarize, the first stage in analysing response suppression is to determine if a regression of *b* against *d* passes through (or close to) the origin. If it does, then the analysis of the ratio *d*/*b* can proceed. Otherwise, the absolute rates *d* and *b* would have to be analysed separately. Whatever the measure used, the appropriate statistical analysis must be used.

6.3. Materials and methods

All of the control and experimental group birds used in the shuttle avoidance experiment were taught to perform an operant response using the operant equipment described in Chapter 3. An operant panel was mounted on a Perspex box (a 'Skinner box'; 0.60m x 0.45m x 0.38m high at the rear, 0.50m high at the front i.e. it had a sloping floor) which was housed in a sound proof wooden box (inside dimensions 1.10m x 0.55m x 0.55m). The box was illuminated by two 15W light bulbs. Four Skinner boxes were constructed, allowing four birds to be 'shaped' (i.e. taught the operant response) simultaneously. An 'auto-shaping' procedure, similar to that originally developed by Brown and Jenkins (1968), was used. This was carried out over a number of one hour sessions. The subject was deprived of food for 24 hours prior to the start of each session. At the end of each session the subject was returned to its home cage and given free access to food for at least 24 hours before being deprived in preparation for the next session.

During the first session, the door in the operant panel was left open. This was to get the birds accustomed to feeding through the doorway. The few birds which did not feed through the doorway during the first session did so during a second session with the door open. At the start of the next session, the door was closed, the key light was not illuminated, and a pellet of food was stuck to the operant key with clear adhesive tape. The operant system was activated to deliver reinforcement (i.e. five seconds access to food) on a fixed ratio one schedule i.e. every peck was reinforced. At intervals of between one and seven minutes, the key light was illuminated for 15 seconds and then the door was opened for 5 seconds. Once the subjects had started to perform the operant response, the reinforcement schedule was switched to variable interval i.e. the first peck to occur after a randomly varied interval was reinforced. The average interval was initially one second, but was increased after every reinforcement by one second until it reached 60 seconds i.e. the interval was randomly varied between 1 and 119 seconds. This was equivalent to a variable interval 1 minute (VI 1) schedule.

All subjects received eight shaping trials over a period of five weeks. At the end of this time, the five subjects from each strain treatment group which performed the highest number of operant responses on the last session were chosen as subjects for the conditioned suppression testing. This resulted in an 2 x 2 experimental design with five subjects in each of the four groups i.e. T-line experimental (TE), S-line experimental (SE), T-line random control (TC) and S-line random control (SC). The subjects retained the same identification number as in the shuttle avoidance experiment.

The birds were tested in a modified shuttle box (Figure 6.2). The food hopper was replaced with an operant panel to facilitate the recording of the operant response rate prior to and during the onset of the warning stimulus. The litter floor in the original box was replaced with a mesh floor. This stopped the birds foraging in the litter for any food pellets which had been dropped during previous trials. A closed circuit television camera mounted above the apparatus allowed the experimenter to observe the subject remotely.

All subjects received a total of ten, one hour sessions. Prior to each session, the subject was deprived of food for 24 hours. At the end of each session, the bird was returned to its home cage and given *ad libitum* access to food for at least 24 hours before being deprived in preparation for the next session.

The first two sessions were simply to accustom the birds to the apparatus, and in particular to feeding from the operant panels in the modified shuttle box. The next four sessions were test sessions; the birds received the same procedures as

in the shuttle avoidance experiment, except the warning light duration was increased to 60 seconds[1], and the average inter-trial interval was increased to 15 minutes (i.e. three warning light exposures per session). The last four sessions were on the extinction schedule i.e. both the experimental and random control groups received three exposures per session to the warning stimulus *only*; the fright was not presented.

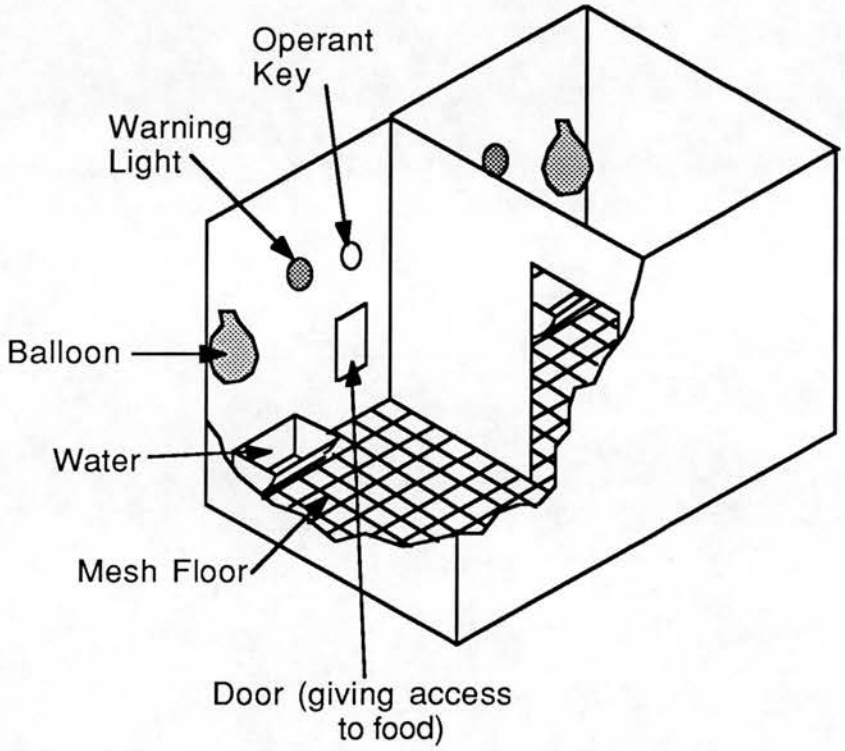

Figure 6.2. The modified shuttle box used in this experiment.

6.4. Results

The raw data (the number of key pecks before and during the warning stimulus and whether or not the bird showed avoidance behaviour) are given in Appendix III.

6.4.1. Shuttle avoidance results

The avoidance results are shown in Figure 6.3. Of the birds which failed to reach the criterion of learning in the shuttle avoidance experiment, two (TE5 and

[1] The increase in warning stimulus duration increased the likelihood of recording a sufficient number of operant responses during the warning stimulus to give a reliable estimate of the subject's general response rate.

SE7) reached a criterion of five successive avoidance trials in this experiment. Of the other four 'non-avoiders', three (SE3, SE4 and SE6) showed little avoidance behaviour, the other one (TE8) avoiding the balloon on ten of the 12 trials, but not reaching the criterion of learning.

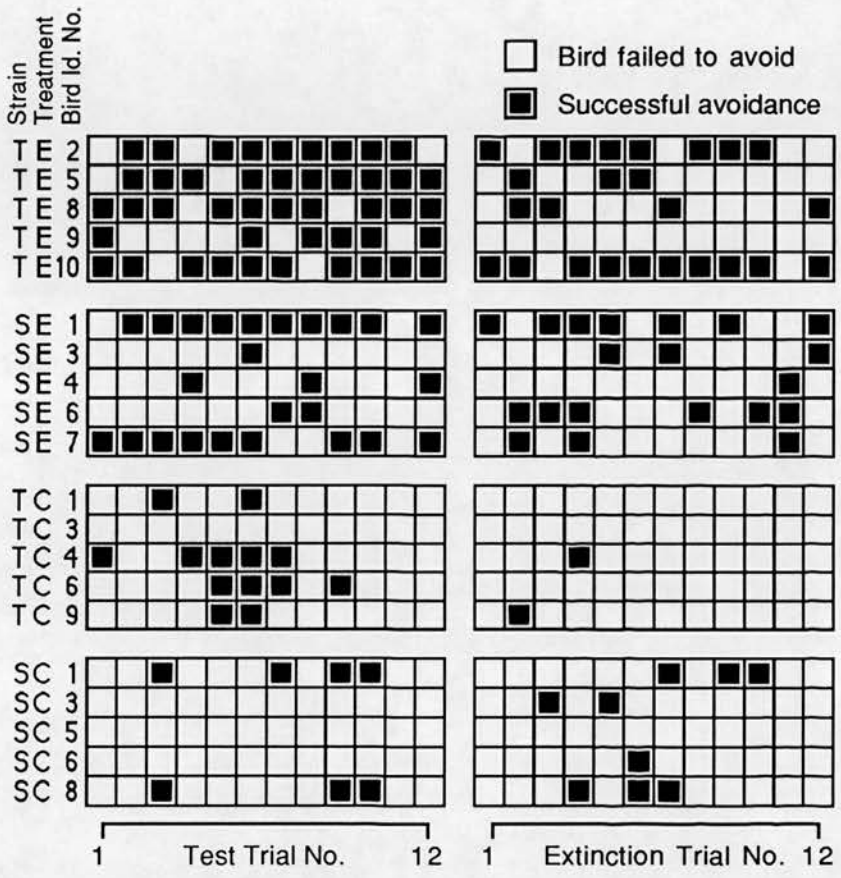

Figure 6.3. Shuttle avoidance responses recorded during the conditioned suppression experiment.

6.4.2. A traditional suppression ratio analysis

The data were also analysed using the traditional suppression ratio i.e. $d/(d+b)$. As pointed out earlier, such an analysis is, strictly speaking, invalid. Such an analysis is, however, useful in so far as it allows results to be compared with those of previous studies. I present it here for comparison, and shall draw no conclusions from it.

Figure 6.4 shows the changes in the mean suppression ratios over the course of the experiment. The suppression ratios were analysed using an Analysis of Variance, and the results of this analysis are given in Table 6.2. Subjects receiving the experimental treatment had a significantly lower suppression ratio than those receiving the random control treatment ($F_{1,16} = 11.94$, $p < 0.01$). The suppression

ratio showed a significant increase from the first to the last session ($F_{7,432} = 9.8$, $p < 0.001$), and there was a significant interaction between the treatment and the session ($F_{7,432} = 2.50$, $p < 0.05$). The strain of the bird did not have a significant effect ($F_{1,16} = 2.40$, $p > 0.10$).

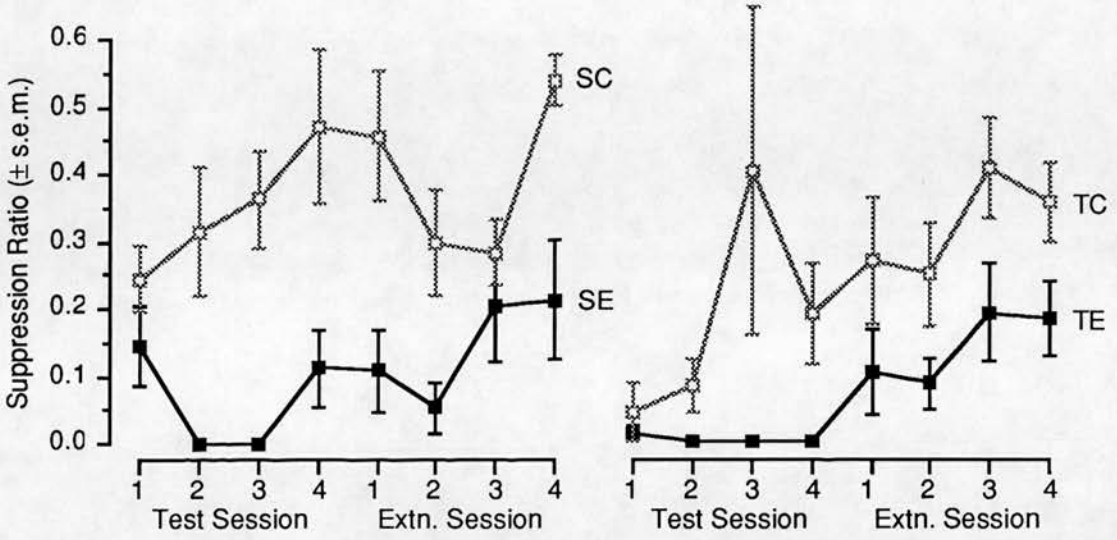

Figure 6.4. The mean suppression ratios (± standard error of the mean) for each group over the eight experimental sessions.

Source of variation	d.f.	s.s.	m.s.	F	p
Between subjects					
Strain	1	0.463	0.463	2.40	
Treatment	1	2.305	2.305	11.94	<0.01
Strain.Treatment	1	0.248	0.248	1.29	
Residual	16	3.089	0.193		
Within subjects					
Session	7	2.228	0.318	9.80	<0.001
Strain.Session	7	0.317	0.045	1.40	
Treatment.Session	7	0.569	0.081	2.50	<0.05
Strain.Treatment.Session	7	0.271	0.039	1.20	
Residual	432	14.024	0.032		
Total	479	23.516			

Table 6.2. Analysis of Variance table for the analysis of the $d/(d+b)$ ratios, taking 0/0 to have a ratio value of 0.00, hence there were no missing values.

6.4.3. Analysis of the ratio d/b

Regression analyses of the rate of responding before the onset of the warning stimulus (*b*) against the rate during the warning stimulus (*d*) are given in Figure 6.5. As these lines had near zero intercepts, the degree of suppression could be calculated as the ratio *d*/*b*. Figure 6.6 shows that there was a very clear relationship between the mean and the variance of this ratio. Although a wide variety of transformations were performed on the data, none was found which could compensate for this. Consequently, parametric analysis using an Analysis of Variance was not possible.

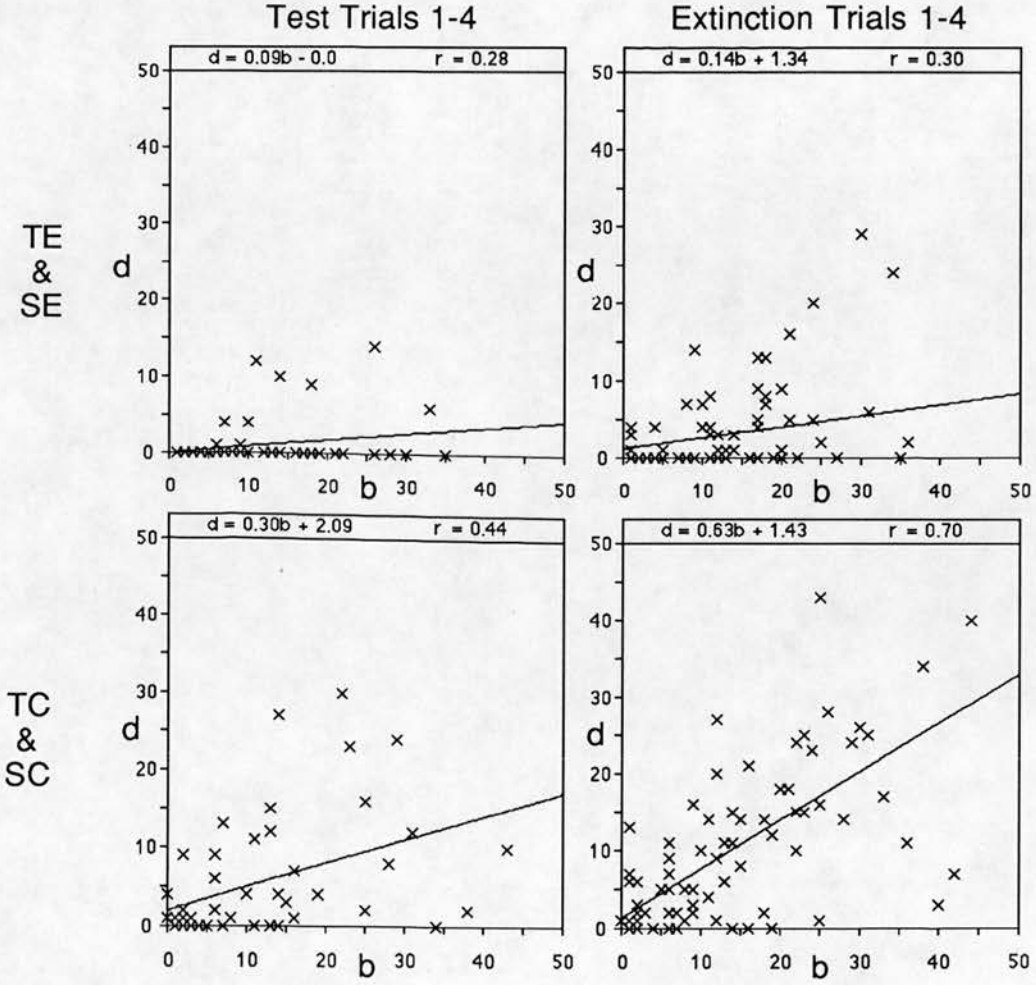

Figure 6.5. Regression analysis of the number of operant responses recorded before (b) and during (d) the warning stimulus. To isolate any treatment or extinction effects, the data were split by treatment and test condition (i.e. testing or extinction).

Figure 6.7 summarizes the response suppression. Trials were divided into three categories: those showing total response suppression (i.e. b=0, d=0), those showing complete conditioned suppression (i.e. b>0, d=0), those showing less than complete conditioned suppression (i.e. b>0, d>0). Total response suppression was shown on exactly half of the testing trials. Given that such trials must be considered as missing data, the statistical analysis of the d/b ratio was abandoned. However, the number of trials on which subjects showed total response suppression was analysed using the Mann-Whitney non-parametric statistical test. There were significantly more total response suppression trials during testing than during extinction ($U_{20,20} = 118.5$, $p < 0.05$), but the number of such trials was unaffected by the strain of the bird ($U_{20,20} = 193$, $p > 0.10$) or the treatment it received ($U_{20,20} = 186$, $p > 0.10$).

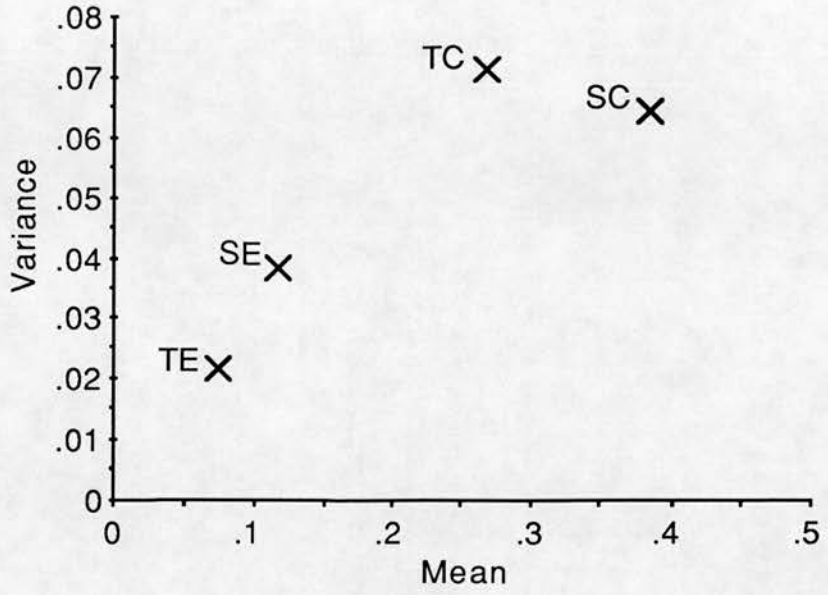

Figure 6.6. Scatter plot of the mean against the variance of the d/b ratio.

To assess the effect of conditioned suppression, the proportion[1] of trials in which the subject showed complete conditioned suppression was analysed using the Mann-Whitney test. The experimental subjects showed a higher proportion of complete conditioned suppression trials than the random controls ($U_{19,20} = 77$, $p <$

[1] This was the proportion of complete conditioned suppression trials out of the trials when b and/or d were greater than zero i.e. it excluded the total response suppression trials, which were taken as missing values. One bird, SC3, showed total response suppression on all of the test trials, and consequently the proportion could not be calculated for this bird during testing. The number of observations in the two sample groups was therefore 19 and 20.

0.01), but this proportion was unaffected by the strain of the bird ($U_{19,20} = 152$, $p > 0.10$) or test condition i.e. test vs extinction trials ($U_{19,20} = 165$, $p > 0.10$).

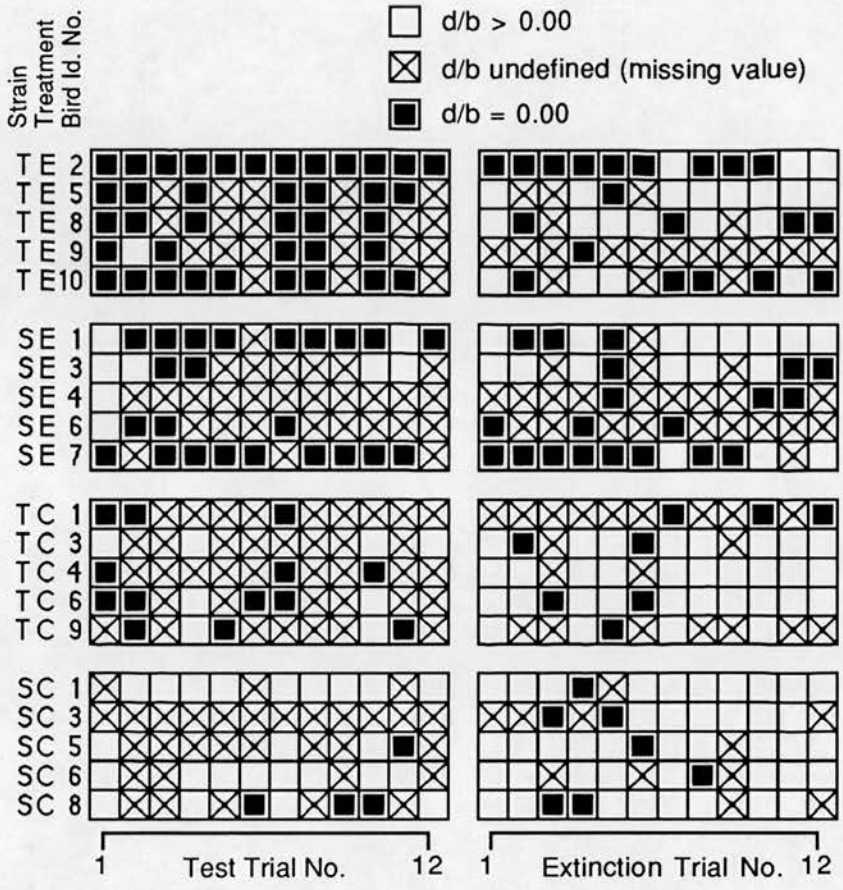

Figure 6.7. A summary of the *d/b* ratios.

6.5. Discussion

Although a full statistical analysis of the data was not possible, the results did reveal a number of features which warrant discussion.

6.5.1. Avoidance behaviour

Two birds (TE5 and SE7) which failed to reach the criterion of learning in the shuttle avoidance experiment did reach it during this experiment. This could have simply been due to them being exposed to further light→balloon pairings. However, this was probably not the case. The majority of birds which failed to learn the shuttle avoidance task had entered the freezing state described in Chapter 5. Once in this state, it usually lasted for the remainder of the experiment. It seems unlikely that that this freezing response would have waned had the shuttle avoidance experiment been continued for a longer period. The effect

appeared to be reinforced by continued exposure to the aversive stimulus and even showed signs of becoming more persistent towards the end of the experiment. The one bird which did stop freezing, SE3, subsequently showed habituation to the balloon in this experiment (described in section 6.5.4). As one might expect, once this bird had habituated to the aversive stimulus it did not make any attempt to avoid it.

It is more likely that the birds which were able to acquire the shuttle response in the experiment reported in this chapter did so as a result of the 9 month 'break' between the two experiments. This allowed the birds to recover from the effects of the experimental treatment, and, in the case of SE7, recover from freezing. Consequently, when these birds were re-tested after this break in the experiment, they were able to acquire the response. This argues in favour of splitting experimental testing over a number of discrete sessions, allowing the subject to recover from the effects of the treatment.

6.5.2. Response suppression and aversion

The response suppression recorded during the experiment fell into two categories. Firstly, there was conditioned suppression, i.e. a reduction in response rate as a result of the onset of the warning stimulus. This was primarily affected by the contingency between the light and the balloon i.e. it was predominantly a feature of the experimental treatment, but was not significantly reduced during extinction. The majority of the conditioned suppression which was recorded during this experiment was complete i.e. the response rate during the warning stimulus was zero. Secondly, there was total response suppression, i.e. the subjects simply stopped responding. This was primarily affected by the presentation of the balloon i.e. there was more total response suppression during testing than during extinction, but it was not affected by the contingency between the light and the balloon.

Investigations into the aversiveness of commercial practices as part of animal welfare research are principally involved with the effects associated with the aversiveness of such stimuli i.e. how frightening they are. Given that total response suppression was affected by the fright (i.e. testing vs extinction) but complete conditioned suppression was not, it appears at first glance that total response suppression may be a better index of aversion than complete conditioned suppression. However, the failure to detect significant differences in conditioned suppression between testing and extinction was probably due to the fact that the

subjects were exposed to relatively few extinction trials. Had there been more extinction trials, the conditioned suppression effect would probably have been lost.

6.5.3. Learning the light→ balloon association

One remarkable feature of the results was the fact that all five of the TE birds showed complete conditioned suppression on the first test trial (an example of which is shown in Figure 6.8), and three of these birds avoided the balloon on that trial. This clearly showed that these birds had still 'remembered' the light→balloon association from the shuttle avoidance experiment, even though the two experiments had been separated by a period of nine months.

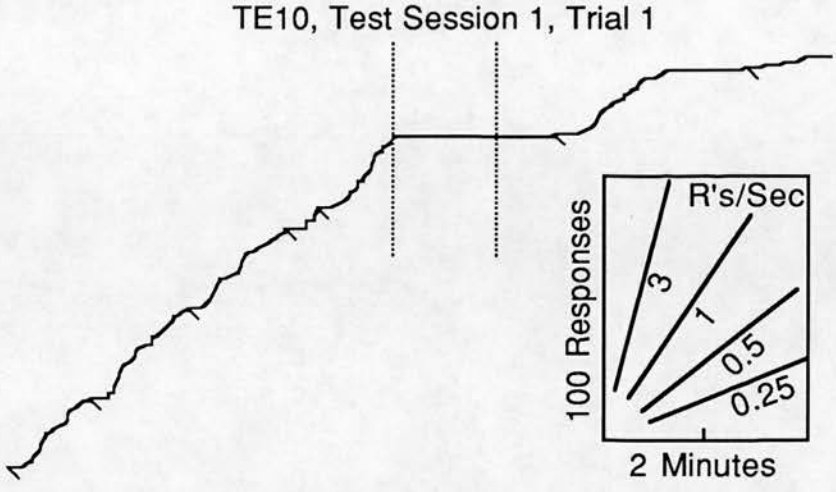

Figure 6.8. Cumulative response record for the first trial received by TE10, showing complete conditioned suppression. (See Chapter 4 for an explanation of cumulative response records.)

In contrast, only one S-line experimental bird, SE7, showed complete conditioned suppression on the first test trial and avoided the balloon on the first test trial. This suggests that the S-lines had not been able to 'remember' the light→balloon association as well as the T-lines. However, the fact that the majority of the S-line experimental birds showed complete conditioned suppression on later trials is proof that they were capable of learning the association between the light and the balloon.

Virtually all of the birds which failed to learn the shuttle avoidance response, either during the shuttle avoidance experiment or during this experiment, showed the conditioned suppression effect on at least one trial. TE8 showed complete conditioned suppression on six test trials, showing total response suppression on

the other six trials. Although SE6 did not show complete conditioned suppression on the first trial, it did on three of the subsequent 11 trials, showing total response suppression on the other test trials. Unfortunately, SE4 showed total response suppression on all but the first trial. Although the total response suppression makes a definite conclusion impossible, these results suggest that the birds which failed to learn the shuttle avoidance task did learn an association between the light and the balloon. However, given that this conclusion is based on a relatively small amount of data from three birds, it must be considered to be tentative.

6.5.4. Habituation to the aversive stimulus

The one bird (SE3) which failed to show conditioned suppression on all but the first of the test trials showed signs of habituating to the balloon. Although this bird showed complete conditioned suppression on test trials three and four, the bird continued to respond during the warning stimulus on trials one and two of the fourth test session (Figure 6.9). By this stage of the experiment the bird had been exposed to the balloon on 32 occasions, and it no longer appeared to be frightened by the balloon. During the second trial on the fourth test session, the bird even continued to feed from the food trough while the balloon was inflating.

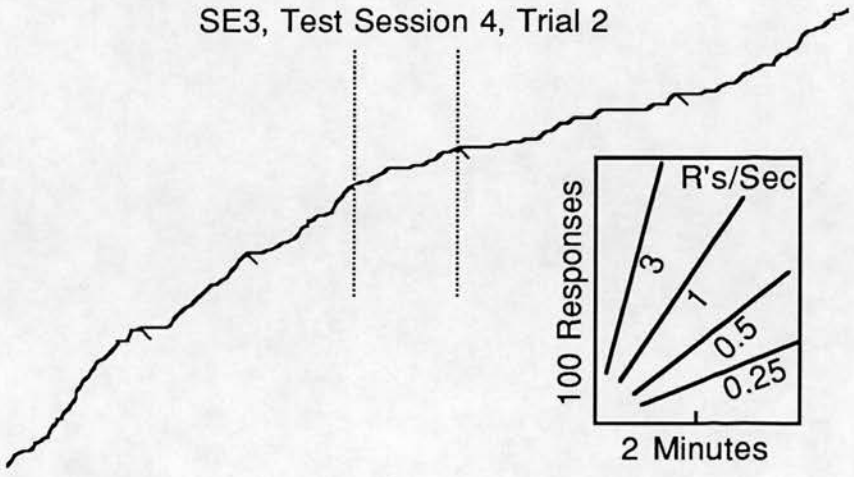

Figure 6.9. Cumulative response record showing signs of habituation in bird SE3.

Although, as discussed in Chapter 3, habituation could confound the measurement of aversion, the habituation recorded in this experiment was almost certainly a result of the extensive exposure to the balloon received in the shuttle avoidance experiment. Had conditioned suppression been measured from the start of conditioning (as opposed to half way through as in this experiment), it is possible that the technique would have been able to discriminate between different

treatments before habituation became a problem. The problem of habituation in conditioned suppression experiments is discussed further in Chapter 8.

6.5.5. The problem of random control group conditioned suppression

Although the random control subjects showed significantly less complete conditioned suppression than those receiving the experimental treatment, the majority of the random control birds, particularly the TC group, showed complete conditioned suppression on at least one trial (an example is shown in Figure 6.10). This suggests that the onset of the warning stimulus caused these birds some 'anxiety', even though the light and the balloon were not explicitly paired. It is possible that the birds found the warning stimulus itself aversive. However the fact that the subjects showed little response to the warning stimulus when first exposed to it in the shuttle avoidance experiment suggests that this was not the case.

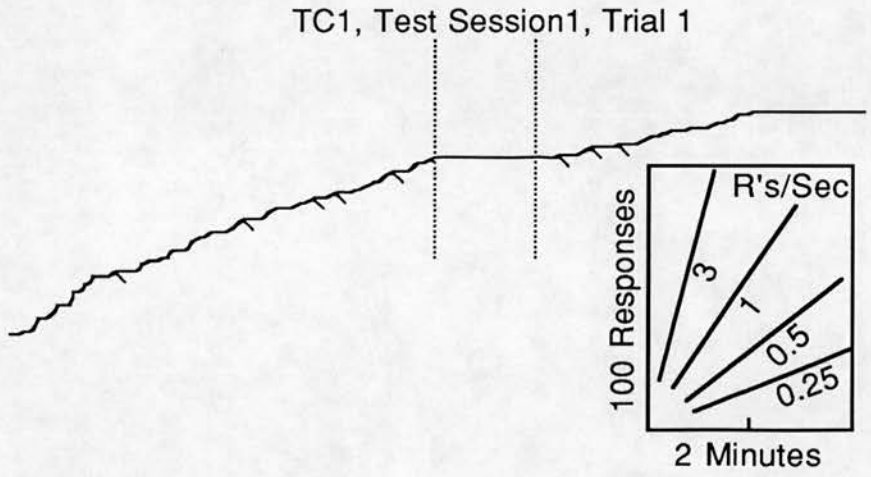

Figure 6.10. Cumulative record showing response suppression in a random control bird.

The development of conditioned suppression without an explicit association between the CS and the US has been noted before in rats (Kremer, 1971; Kremer and Kamin, 1971; Quinsey, 1971). One possible explanation for this is that the truly random control procedure is "restrictive only in regards to stimulus contingencies, and therefore, coincident occurrences of the CS and US can and do occur" (Kremer, 1974). However, given the relatively long inter-trial intervals and short warning stimulus durations used in this experiment, coincident occurrences of the light and balloon were very rare. Each random control subject received an average of only 0.65 light→balloon pairings, and any one individual receiving no

more than two pairings during all of the test trials. It is, therefore, unlikely that such a minimal number of direct pairings of the light and balloon could account for the suppressive effects of the warning stimulus.

An alternative explanation for the random control group suppression is that it was due to the subjects forming a *general* association between the light and the balloon. In the current study, the birds initially received exposure to the light, balloon and shuttle box in the shuttle avoidance experiment. Consequently, they may have formed a general association between all three. During the first two sessions in the modified shuttle box during this experiment, neither the balloon nor the light were presented. During session three, the birds received three exposures to the balloon and three to the light. Given that the birds were only ever exposed to the light and the balloon in the test situation, they may have formed a general association between the light, the balloon and the box.

This finding questions the validity of the truly random control procedure, particularly in studies oriented towards welfare research. Rescorla (1967) originally proposed the truly random control to overcome what he saw as the inadequacies of the traditional control techniques. As a psychologist interested in learning, Rescorla was primarily interested in the association between the CS and the US. In a psychologist's learning experiment, the purpose of the control is to ensure that any differences in behaviour are due to this CS→US association. In such a context, Rescorla's truly random control is quite appropriate, and other control procedures (e.g. presenting either the CS only, the US only, or presenting the CS and US such that they are explicitly unpaired) are inadequate (Rescorla, 1967). However, the principal aim of the study reported in this thesis is to assess the aversiveness of the US. In such a context, the purpose of the control is to ensure that any changes in behaviour are due to the US and not simply to the CS. Under these circumstances, the truly random control is inadequate in that it does not allow CS effects to be isolated. However, one of the control techniques rejected by Rescorla *is* suitable for studies primarily interested in the aversiveness of the US. This is the CS only control, with which "any differences between *S*s [subjects] can be attributed to this difference in experience with the US" (Rescorla, 1967). Consequently, I propose that *the CS only control should be used* when aversion learning techniques are used for welfare assessment.

This again highlights the problem of the difference of interest between those implementing aversion learning techniques to assess animal welfare and those using them to study learning, and further justifies the work presented in this thesis.

6.5.6. The problem of total response suppression

The main cause of the difficulty of analysing the suppression results was the total response suppression (i.e. b=0, d=0) which occurred on at least one trial for all but one subject. Examination of the cumulative response records showed a number of likely causes. Figure 6.11 shows a typical cumulative record for the last habituation session and all of the test and extinction sessions for one subject.

At least some of the total response suppression trials were probably due to the comparatively long duration of each session. When first placed into the box, the birds would immediately start to perform the operant response. However, as the top record (H3) in Figure 6.11 shows, the operant response rate would typically fall to zero about half way through the session. This was probably due to satiety, with the food received during the numerous reinforcements filling the bird's crop so that it could not eat any more. As a result, the bird was no longer motivated to perform the response, and so no responses were recorded either in the minute before or during the last trial in the session. This was a common problem, with the majority of subjects showing the effect (shown in Figure 6.7 by the high proportion of Xs on every third trial).

The problem of satiety could be overcome in a number of ways. Firstly, the duration of each session could be halved so that the bird would be responding during most of the session. However, in order to keep a similar inter-trial interval, the number of trials per session would have to be reduced. In order to present the same number of trials, the number of sessions would, therefore, have to be increased, increasing the total time taken to perform the experiment. A better solution would be to halve the duration of the reward so that the birds could not eat as much food. Alternatively, the schedule interval could be increased from variable interval one minute to variable interval two minutes so that the birds would, on average, receive reinforcement half as often. Although these two solutions would almost certainly require the subjects to undergo more initial training, they would probably solve the satiety problem without a significant increase in the duration of the experiment.

Exposure to the balloon also had a significant effect on the occurrence of complete operant suppression trials. As the second record (T1) in Figure 6.11 shows, operant responding virtually stopped after the first fright during the first session, and the bird performed hardly any operant responses during the subsequent test trials (T2-T4). Once exposure to the balloon stopped i.e. during

the extinction sessions, operant responding recovered, with the response rate returning to pre-test levels on the fourth of these sessions.

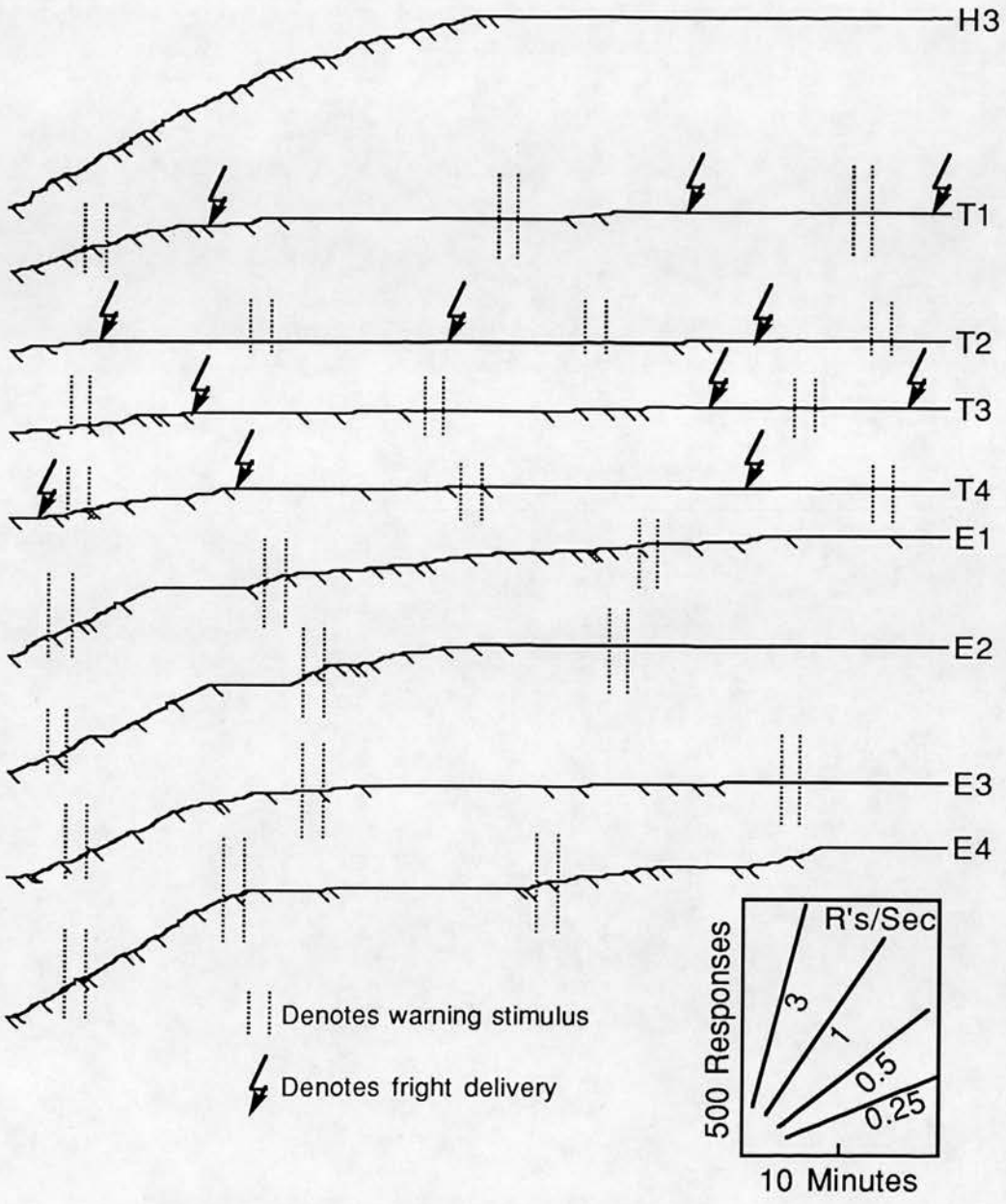

Figure 6.11. Cumulative response record for one subject (SC5) for the last habituation session (H3), the four test sessions (T1-T4) and the four extinction sessions (E1-E4). Note that only the first 47 minutes of each session are shown. No responses were recorded in the last 13 minutes of any session.

Given that the development of total response suppression is associated with the fright, it could be used as an indicator of the aversiveness of the stimulus.

However, as this experiment showed, the phenomenon can develop very rapidly, and might not show much discrimination between different levels of aversion.

The fact that the response rate at the start of the second test day was low even before the bird had received a fright suggests that there was also an indirect response suppression effect related to the fright. Given that the subjects only received exposure to the balloon in the shuttle box, it is possible that the subjects associated the experimental apparatus with the aversive stimulus. The subjects then came to fear the apparatus, and the birds' behaviour (including operant behaviour) was generally suppressed when they were placed in the box. This phenomenon has been noted before in rats (e.g. Kremer, 1974). Alternatively, it is possible that the birds superstitiously associated operant responding with the aversive event i.e. that they perceived that the fright was contingent on their responding. Consequently, the birds would have stopped performing a response which they perceived as being punished. The fact that the birds still received frights even when they did not respond should have eliminated such an association. However, the fact that each subject was tested over a large number of discrete trials may have enhanced the general suppressive effects due to any superstitious association. Each session started with the bird being deprived of food for 24 hours and being placed into either the Skinner box during shaping, or the modified shuttle box for testing. At the end of the one hour period in the experimental apparatus, the subject was returned to its 'home' cage where it was given free access to food. Given the large number of shaping, training and habituation sessions, the conditions existed for the birds to learn the general experimental procedure i.e. a long period of food deprivation followed by a short spell in some apparatus followed by return to the 'home' cage where it could feed. If the birds had learnt this sequence of events, they had little to lose by not responding when placed in the apparatus as they may have learnt that they would be returned to their 'home' cage at the end of the session. Therefore, any indication of an association between key pecking and the occurrence of the balloon may have been enough to suppress such behaviour.

Perhaps the simplest way to overcome these problems would be to make the test cage the subjects 'home' cage, with food only being available through the operant panel. This would ensure that the birds would be less likely to give up operant responding as it would be their only means of gaining access to food. However, if the birds were on a simple free-operant schedule i.e. the reinforcement schedule was active all of the time, the birds would probably only be performing the operant response for a limited period each day. It would, therefore, be likely that

the majority of warning stimulus presentations would occur when the bird was not performing the response, resulting in an even higher proportion of total response suppression trials than a discrete session approach. This could, of course, be overcome by only presenting the warning stimulus when the bird *is* responding. However, the paradigm is then no longer truly classical. As warning stimulus presentation is now contingent on the subject performing the operant response, it is an example of conditioned punishment, similar to a procedure developed by Hake and Azrin (1965). An experiment investigating a response-contingent fright technique is described in detail in Chapter 8, and the relative merits of contingent vs non-contingent fright techniques are discussed in that chapter.

Alternatively, the problems of a free-operant approach could be overcome by using a discriminative operant procedure i.e. the operant schedule would only become active during certain periods of the day, these being signalled by the presentation of some discriminative stimulus (S^D). However, the design of a conditioned suppression experiment which utilized discriminative operant responding would need to ensure that it did not contain a contingency between the discriminative stimulus and the CS. For example, if the CS was presented during each presentation of the S^D, the S^D would act as a secondary CS signalling the onset of the primary CS, which itself signals the aversive event. The S^D could, therefore, result in some response suppression itself if the subject were to associate it with the presentation of the aversive stimulus. This contingency could only be avoided by presenting the CS in a pseudo random manner, such that some CS presentations occurred during some of the S^D trials, some S^D trials were without CS presentations, and some CS presentations occurred in the intervals between the S^D trials. However, this would once again result in a proportion of trials in which the effects of the CS could not be measured because the subject is not performing an operant response when the CS comes on.

6.5.7. The problem of complete conditioned suppression

Whereas the complete conditioned suppression (i.e. $b>0$, $d=0$) clearly demonstrates that the 'aversive stimulus' is indeed aversive, such complete suppression makes it difficult to differentiate between different levels of aversion. Once the response rate during the warning stimulus drops to zero, the level of aversion experienced by the subject has essentially dropped off the bottom of the scale which is being used to measure aversion. Therefore, once the response rate reaches zero, the technique can no longer discriminate between different levels of aversion. The initial frantic escape activity shown by the birds in the shuttle

avoidance experiment suggests that the inflating balloon was a very potent aversive stimulus. The aversiveness of some of the commercial procedures which might be investigated with a conditioned suppression technique would probably be lower than the balloon. These less aversive stimuli would probably not result in complete conditioned suppression and consequently discrimination of different levels of aversion resulting from these procedures would be possible. However, a few commercial practices may be at least as aversive as the balloon, and would, therefore, result in complete conditioned suppression.

One of the problems with the current experiment was the fact that it started after the majority of the experimental subjects had learnt the association between the light and the balloon. There is, however, no reason why conditioned suppression could not be recorded while the subject learns the CS→U S association. Had response suppression been recorded from the first pairing of the light and the balloon, intermediate levels of response suppression (i.e. $b > d > 0$) may have been observed. However, classically conditioned associations can be learnt after relatively few trials, resulting in rapid development of total operant suppression during the CS. This could be overcome by recording the *recovery* of responding when the CS is presented during extinction i.e. when the US no longer follows the CS[1] . This is probably the most promising approach, although if the stimulus is very aversive, it may take a considerable number of no-fright trials before the subject stops showing complete conditioned suppression.

The probability of the US following the CS has been shown to affect the degree of suppression. Willis and Lundin (1966) found that rats showed greater conditioned suppression when there was a 90% probability of the US following the CS, compared to when there was a just a 10% probability. Indeed, it may be possible to vary the CS→US probability so as to obtain a fixed degree of suppression e.g. 50% of the baseline rate. The probability value itself could then be used as the measure of aversion: the lower the probability needed to induce the required suppression the more aversive the stimuli. However, this would be very difficult to achieve in practice, unless each subject received extensive testing over a large number of trials.

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[1] Traditionally, this method has involved the presentation of the CS only. Rescorla (1967) argued that the truly random control procedure i.e. the presentation of the CS and US completely at random, was also the correct extinction procedure. However, given the problems associated with the truly random control (discussed previously), the CS only extinction procedure is preferable.

A more practical proposition would be to use a fixed probability (e.g. have the US follow the CS on 25% of the CS presentations) in order to reduce response suppression to a level at which discrimination is possible. The exact probability level would have to be obtained after a pilot study using a number of different probabilities. The chosen level would have to be such that the most aversive stimulus being tested did not produce complete conditioned suppression, but the least aversive one produced some conditioned suppression. This may not be possible, and two or more probabilities may have to be used, with some treatments being tested under the two (or more) probabilities to allow comparisons between the various groups and/or treatments.

Reducing the CS→US probability has the added bonus of increasing the resistance to extinction of conditioned suppression (Brimmer and Dockrill, 1966). Lower extinction rates would probably allow greater discrimination between different levels of aversion. However, this advantage may be lost given that a 50% probability of the US following the CS results in suppression ratios having a greater variance than with a 90% CS→US probability (Willis and Lundin, 1966).

6.6. Conclusion

The length of the discussion is testament to the problems encountered in this experiment. Although many of the problems could be overcome by designing a conditioned suppression technique which incorporated some of the suggested solutions, some fundamental problems with non-contingent aversive reinforcement come to light when it is compared with response contingent reinforcement. Consequently, the suitability or otherwise of conditioned suppression for welfare assessment will be deferred until these are discussed in Chapter 8.

CHAPTER 7 One-Way Avoidance

7.1. Introduction

Approximately half of the subjects tested in the shuttle avoidance experiment (described in Chapter 5) failed to learn the shuttle avoidance task. A one-way avoidance task i.e. one in which the subjects have only to run in one direction, rather than two, in order to avoid is generally easier to learn (Brush, 1966; Bolles, 1970). For example, Theios and Dunaway (1964) demonstrated that rats needed approximately 70 trials in order to learn a shuttle avoidance task, whereas a one-way avoidance task was learnt after only approximately 15 trials.

Unfortunately, the one-way nature of the task imposes a practical problem: how to get the subject back into the location where the shock occurs. Traditionally, the subject was simply picked up by the experimenter and then dropped back into the shock compartment. However, as discussed earlier, this extra handling could seriously confound the measurement of any aversion caused by the experimental treatment. This consideration is of particular importance when using the technique to assess the aversiveness of commercial husbandry practices, where the human operator is probably an important component of the aversive stimulus (Jones, Duncan and Hughes, 1981).

Davis, Babbini and Huneycutt (1967) overcame this problem by devising a four compartment one-way avoidance box. The four compartments were arranged in a square and were separated by sliding doors (Figure 7.1). At the start of the experiment the rat was placed in compartment A. The CS consisted of sounding a buzzer and the raising of the door between the compartment that the rat was in and the next compartment (i.e. B). If after seven seconds the rat had not moved into B, it received a shock (of unspecified intensity and duration). On the next trial, the door between compartments B and C was raised, and the rat had to run into C in order to avoid the shock. This cycle was repeated in subsequent trials, with the subject moving through the four compartments, trial by trial, in a clockwise

direction. Although the subject eventually entered compartments where it had previously received a shock, it never had to enter one where this had only just happened (i.e. in the preceding trial). Rats tested in this way show significantly more avoidance behaviour than subjects taught a shuttle response between two of the four compartments (Davis *et al*, 1967). Consequently, the apparatus allows the use of the comparatively easily learnt one-way avoidance task without the need to handle subjects between trials.

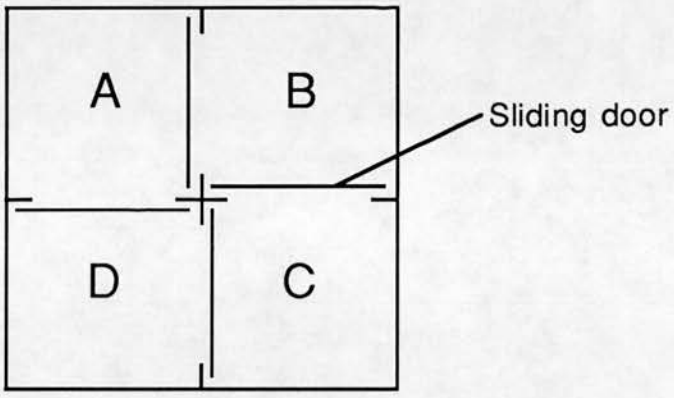

Figure 7.1. The one-way avoidance apparatus devised by Davis *et al* (1967).

Given the poor avoidance performance observed in the shuttle avoidance experiment, the aim of this experiment was to determine if domestic fowl could learn a one-way avoidance task.

7.2. Materials and methods

The subjects were tested in a one-way avoidance box, similar to that developed by Davis *et al* (1967). The box consisted of four compartments (0.41 m x 0.41 m x 0.41 m) arranged in a square (Figure 7.2). The outer two walls of each compartment were formed by two commercial battery cage fronts (Figure 7.3). The inner two walls were formed by two solid sliding doors (0.36 m x 0.41 m). One side of each door was painted white, the other side black, so that each compartment had one black and one white door (Figure 7.3). Each compartment could be illuminated separately by a lamp (240V AC, 100W) from above, and each had a food and water trough. Partitions between each compartment ensured that the subject could not look into adjacent compartments. The four compartments were surrounded by a screen which allowed the experimenter to observe the subject (through a peep-hole), to control the doors separating each compartment and to take up a position ready to deliver the aversive stimulus without being seen by the subject.

For the experimental treatment, the warning stimulus comprised simultaneously raising the door to the next compartment, sounding a buzzer and switching the light source such that only the next compartment became illuminated. This caused the light intensity in the first compartment to fall from the illuminated level of 700 lux to a level of 50 lux. If after ten seconds the subject had not moved into the other compartment, the bird received the aversive stimulus. This consisted of the experimenter 'dusting' the cage compartment the bird was in with a large feather duster. This procedure was designed to mimic the commercial practice of cage dusting. The cage was dusted until the bird had escaped into the next compartment and the door was lowered behind it. If the bird moved into the other compartment before the end of the warning stimulus (the avoidance response) the door was immediately lowered behind it and the compartment was not dusted. General qualitative observations about the birds' behaviour were also noted.

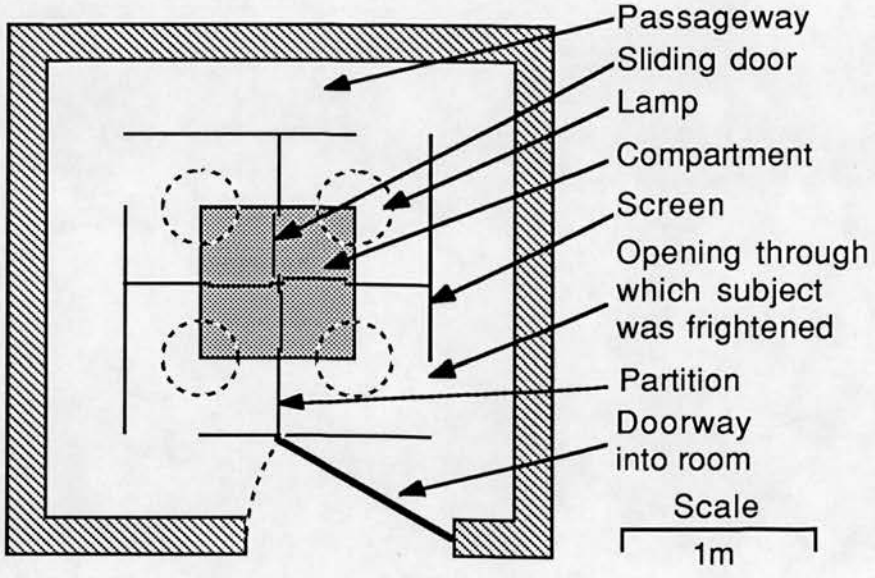

Figure 7.2. Plan view of the one-way apparatus.

It is possible that the birds moved into the adjacent cage for some reason other than avoiding the fright. For example, the birds might have wanted to explore the new cage, or may have been attracted into it because it was illuminated. A second group was, therefore, subjected to a control treatment. This involved presenting the warning stimulus alone, i.e. the control birds received no frights. This 'no fright' control was used in preference to the truly random control for the reasons given in Chapter 6. If the subject moved into the next cage during the stimulus presentation, the door was closed behind it and the bird was recorded as having shown an 'avoidance' response. If, when the warning stimulus had finished,

the bird had not moved into the other cage, the door was lowered and the light source was switched back to illuminate the cage the bird was in.

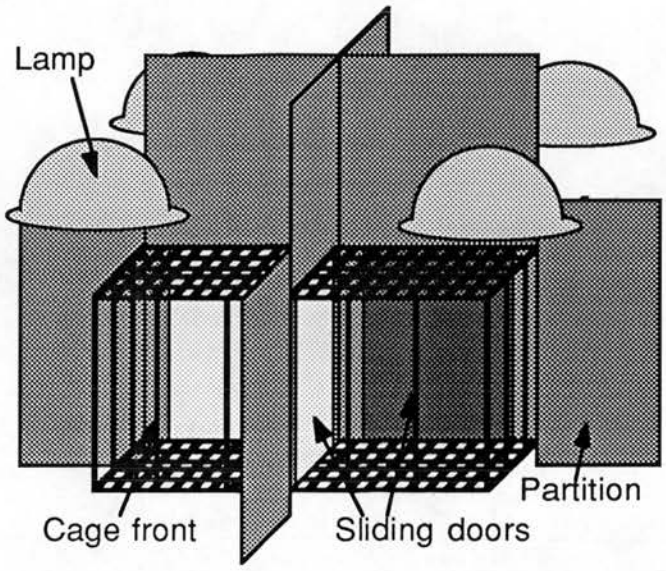

Figure 7.3. Detailed view of the central part of the one-way apparatus.

As in the previous experiments, the generality of the procedure was tested by using two strains of hens; the S-line and T-line strains described in Chapter 5. Five birds of each strain received the experimental treatment and five the control treatment. This resulted in a 2 x 2 design, with four groups: T-line experimental (TE), S-line experimental (SE), T-line control (TC) and S-line control (SC). It is possible that the direction in which the birds were required to move around the apparatus would influence avoidance performance. Therefore, half of the subjects were required to move in a clockwise direction and half in an anti-clockwise direction. The required direction was pseudo-randomly assigned to subjects so as to partition the direction equally within both of the main effects, i.e. five birds of each strain and treatment had to move in a clockwise direction and five in an anti-clockwise direction.

Each bird was tested in a single eight hour session for a total of 48 trials. The inter-trial interval was randomly varied from five to 15 minutes. The birds were placed in the apparatus 15 minutes before testing began.

7.3. Results

The results are summarized in Figure 7.4, and shown in full in Figure 7.5. All of the birds which received the experimental treatment showed avoidance behaviour on at least eight out of the last ten trials.

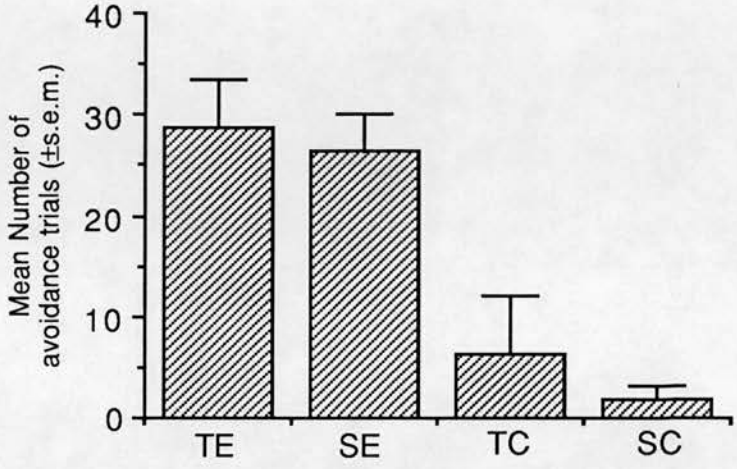

Figure 7.4. Histogram showing the mean number of avoidance responses shown by each of the four groups.

Although the variance of the data was not strictly homogeneous, the main treatment effect was large enough to ensure that an Analysis of Variance would not have been compromised. The number of avoidance trials shown by each subject was, therefore, analysed using an Analysis of Variance and the results of this analysis are given in Table 7.1. Subjects receiving the experimental treatment showed significantly more avoidance responses than those receiving the control treatment ($F_{1,12} = 45.27$, $p < 0.001$). Subjects required to move around the apparatus in an anti-clockwise direction showed significantly more avoidance responses than those having to move in a clockwise direction ($F_{1,12} = 9.38$, $p < 0.01$). The strain of the bird did not have a significant effect ($F_{1,12} = 1.00$, $p > 0.10$), nor were there any significant interactions between treatment, strain and the direction in which the birds were tested (Table 7.1).

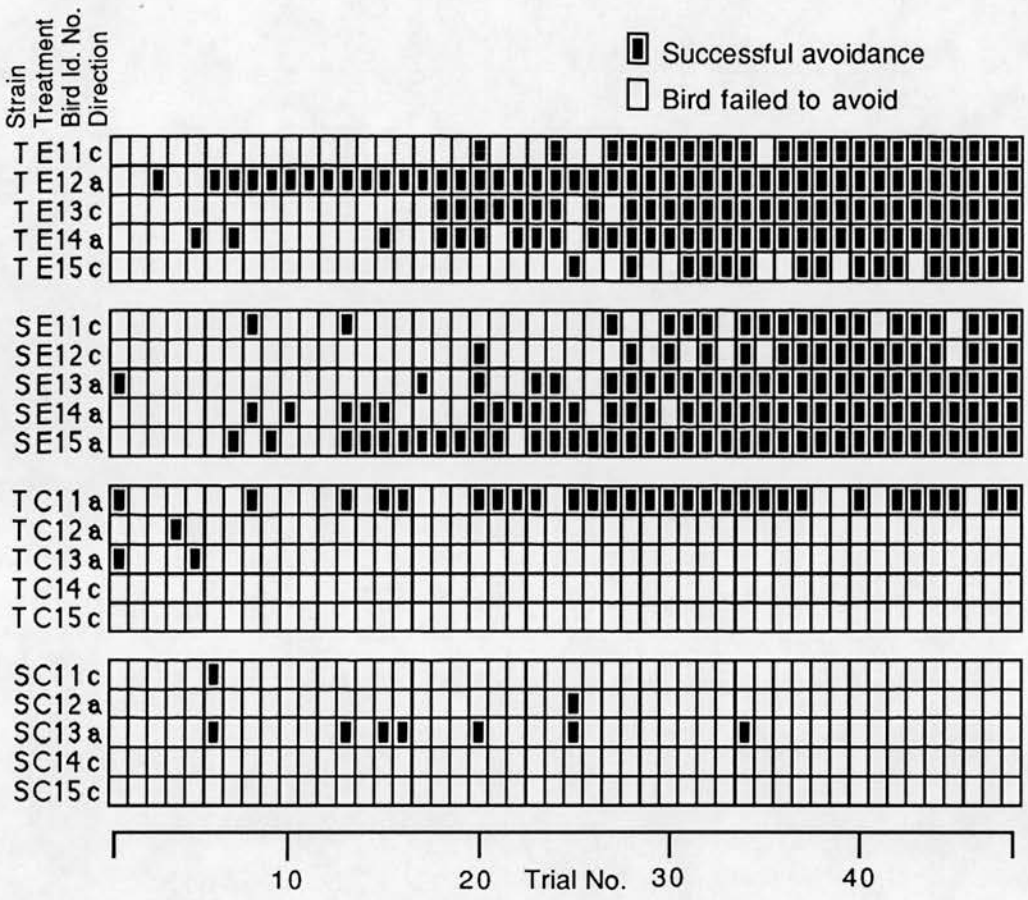

Figure 7.5. One-way avoidance results.

Source of variation	d.f.	s.s.	m.s.	F	p
Strain	1	61.25	61.25	1.00	
Treatment	1	2761.25	2761.25	45.27	<0.001
Direction	1	572.45	572.45	9.38	<0.01
Strain.Treatment	1	5.63	5.63	0.09	
Strain.Direction	1	20.83	20.83	0.34	
Treatment.Direction	1	67.50	67.50	1.11	
Strain.Treatment.Direction	1	9.63	9.63	0.16	
Residual	12	732.00	61.00		
Total	19	4230.55			

Table 7.1. One-way avoidance Analysis of Variance table .

7.4. Discussion

Generally, the one-way avoidance response was learnt by all of the birds receiving the experimental treatment and regardless of strain. There was, however, a big variation between individuals in the number of avoidance responses shown during the 48 trials. One bird (TE12) avoided the fright on 44 out of the 48

trials, whilst another (TE15) showed avoidance behaviour on only 16. As one might expect, the non-avoidance trials were generally in the earlier part of the session. Once the subjects started to show avoidance behaviour it generally continued for the remainder of the experiment. On average, each experimental subject received 20.4 frights over the 48 trials. Such extensive exposure to the aversive stimulus could lead to the problem of habituation, which, as was pointed out in Chapter 3, can confound the measurement of aversion.

The control birds generally showed little or no avoidance. There was one exception to this; TC11 showed avoidance behaviour on 29 trials. The fact that a no-fright control showed either the same or more avoidance behaviour than half of the experimental subjects could indicate that the experimental birds were not showing 'true' avoidance. However, TC11 alarm called during the majority of the 48 trials, suggesting that it was frightened by some component of the test situation. Often, the alarm calling would begin *before* the warning stimulus came on. Although the experimenter could enter the test room and take position behind the screen without being seen by the bird, any noise the experimenter made could be detected by the bird. It is, therefore, possible that TC11 was particularly sensitive to such noise, and it may have acted as a potent enough aversive stimulus to initiate avoidance. Although the experimenter left the room immediately after each trial irrespective of the bird's behaviour, the bird may have superstitiously associated the avoidance response with the experimenter leaving the room.

The avoidance behaviour shown by TC11 began to decrease towards the end of the session. Indeed, the bird failed to show an avoidance response on four of the last ten trials, compared to a mean of 0.05 non-avoidance trials out of ten for the experimental subjects. This was probably due to the bird habituating to whatever stimulus it found aversive, suggesting that whatever the stimulus was, it was mild.

7.4.1. The direction effect

The significant 'direction of avoidance' effect is difficult to explain. Why should birds moving in an anti-clockwise direction show more avoidance than those moving in a clockwise direction? The effect probably has little to do with the actual direction of avoidance. If the effect is real (as opposed to a statistical anomaly), it may be associated with the colour of the doors. As described earlier, the sliding doors were painted matt white on one side and matt black on the other, such that each compartment had one white door and one black one. Birds which moved around the apparatus in a clockwise direction moved out of the cage through a

white door, and those which moved anti-clockwise through a black door. The question then becomes why should birds moving through a black door show more avoidance than those moving through a white door?

One possible explanation for this is that the birds moving through a black door entered a compartment which had another matt black door, and this may have looked like an opening into another cage. Therefore, the birds believed that they were escaping into a cage which was larger that the actual size of the compartment. The birds moving through the white door moved into a compartment with another white door which may have looked like a solid wall. Consequently, these birds may have perceived the cage for what it was - a relatively small compartment. This ties in with the 'effectiveness of escape' theory proposed in Chapter 5. The birds moving through the black door perceived an avoidance/escape response into the larger cage as a more effective response than those birds avoiding/escaping into a cage with a white door. Consequently, birds moving through a black door were more likely to perform an avoidance response, hence the 'direction' effect. Of course once the birds had performed the response a few times they probably realized that the black door was actually a door. However, the increase in the perceived effectiveness of the escape response would have occurred during the critical first few trials. Once the birds had learnt the avoidance response it generally continued for the remainder of the experiment.

Although this is plausible, I suggest that the direction effect is a statistical anomaly and not biologically significant. The fact that one control bird which showed avoidance behaviour (TC11) moved in an anti-clockwise direction was probably enough to weight the results and yield a statistically significant effect. Of course the only way to prove this would be to repeat the experiment, having door colour and direction as the main effects i.e. some birds moving clockwise through black doors, some anti-clockwise through black doors, some clockwise through white doors and some anti-clockwise through white doors.

7.4.2. One-way vs shuttle avoidance

Superficially, it appears that the one-way avoidance experiment was far more successful than the shuttle avoidance experiment; all of the one-way experimental subjects 'learnt' the avoidance response and there was no strain difference. However, the relative success of the one-way task was possibly due to the sheer number of trials to which each subject was exposed. Had the experiment been performed under the same paradigm as the shuttle avoidance experiment (i.e. test to a criterion of five consecutive avoidance trials or to a maximum of 30 trials), the

results would have been quite different (Figure 7.6). In this case, only half of the experimental group would have reached the criterion of learning. Indeed, there is no significant difference ($U_{10,20} = 166$, $p > 0.1$) in the avoidance performance of the shuttle avoidance experimental birds compared with the one-way avoidance experimental birds had the latter been tested to the shuttle avoidance criterion.[1]

It is therefore possible that had the shuttle avoidance experiment continued for 48 trials, the majority of the experimental subjects would have learnt the avoidance response. However, as was discussed in Chapters 5 and 6, the persistence of the freezing response shown by the majority of the non-avoiders would probably have meant that this would not have been the case.

The experimental procedure in this experiment was designed to prevent freezing behaviour. The experimenter continued to frighten the subject until it did escape. Although some subjects initially froze when the cage was first dusted, the birds invariably fled into the next compartment within five seconds exposure to the aversive stimulus. In the shuttle avoidance experiment, the termination of the aversive stimulus i.e. the slow deflation of the balloon, occurred irrespective of the bird's response. Although the birds could escape from the balloon by fleeing into the other compartment, they could also 'escape' it by freezing (as discussed in Chapter 5). It was probably this punishment of freezing in the one-way avoidance experiment which, above all else, accounted for all the experimental subjects learning the one-way avoidance response. This could be tested by repeating the one-way avoidance experiment with two groups, one exposed to a short fixed

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[1]This was tested using the same analysis procedure as in the shuttle avoidance experiment. Those birds which reached the criterion of learning were ranked according to the number of trials needed to reach the criterion. The remaining birds were then ranked below the 'avoiders', according to the proportion of trials on which they showed the avoidance response. These ranks were analysed using the Mann-Whitney non-parametric statistical test.

Such a comparison is, statistically speaking, invalid because such an analysis is based upon one variable i.e. the whole experimental paradigm. This one variable was made up of a number of different variables i.e. type of aversive stimulus, warning stimulus type, duration and timing of the experiment etc. It is possible that there were significant but opposite effects within these variables which, when combined into the single variable cancelled out. The results of this analysis must, therefore, be treated with caution.

The best way to compare one-way and shuttle avoidance would be to repeat the experiment with one group of subjects required to perform a one-way avoidance response round all four compartments, and another group performing a shuttle response between two of the compartments. Davis *et al* (1967) did just this and found that rats learnt the one-way avoidance task more readily than the shuttle avoidance task.

duration fright, and subjects in the other being frightened until they escaped. If this hypothesis is correct, the birds being frightened until they escaped would show more avoidance that those receiving the fixed duration fright.

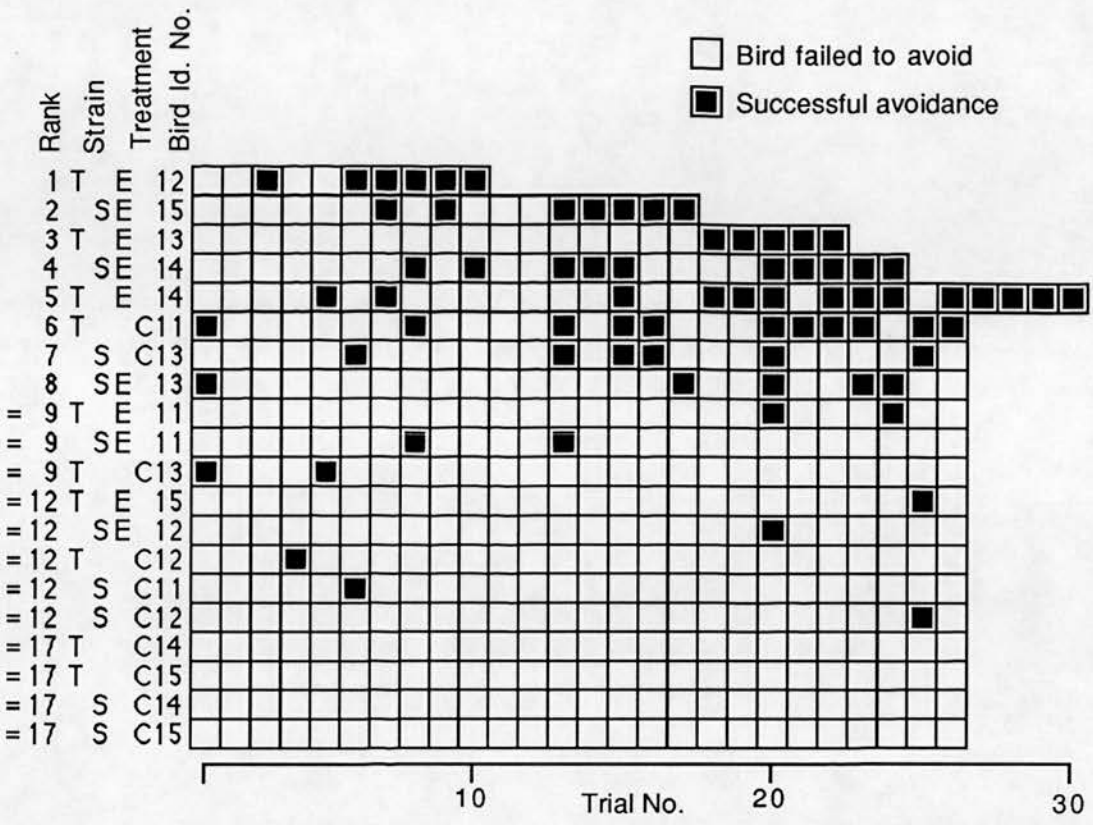

Figure 7.6. The one-way avoidance results had the experiment been performed to the criterion of learning used in the shuttle avoidance experiment.

The perceived effectiveness of the one-way avoidance response may also have contributed to it being more readily acquired than the shuttle avoidance response. The shuttle response usually requires the subject to move into a compartment where it had been frightened on the previous trial; there is no one place in the box which is always safe. In contrast, in a 'true' one-way avoidance experiment, the subject receives aversive stimulation in one compartment, but never in the other. One side of the box is always safe. Although the subject would probably 'want' to put more distance between itself and the aversive stimulus, a one way avoidance response does at least take the animal to a safe place, and is, therefore, effective in that sense. The shuttle response, however, is not very effective in that it does not even take the subject to a place which is always safe.

The one-way apparatus used in this experiment involves a response which lies between the 'true' one-way and shuttle responses. Although the response

took the bird into a compartment which was never the one where it had just been frightened, on the fourth trial the bird did move into a place where it had previously been frightened. It is difficult tell whether the birds perceived the apparatus as four compartments arranged in a circle, or whether they perceived each compartment as being 'new'. The avoidance performance recorded by Davis *et al* (1967) in their apparatus was acquired more readily (i.e. after fewer trials) than a shuttle task, but was not as readily acquired as a true one-way task. This suggests that the subjects did not perceive each compartment as new, safe place. However, as Davis *et al* (1967) point out, "reaching a distinct safety point or being handled after the response can become powerful conditioned reinforcers". Similarity between the compartments in a two compartment one-way avoidance task has been shown to retard avoidance training (Knapp,1965), and may have accounted for the comparatively slow acquisition in the four compartment box compared to a true one-way response.

7.5. Conclusion

Although both strains of hen learnt this one-way avoidance task, the relatively high average number of frights that subjects received before this happened could lead to problems with habituation if the technique were used with a less aversive stimulus. Consequently, although the technique passes the first criterion, it fails to meet the second criterion stipulated in Chapter 3. One-way avoidance *cannot*, therefore, be recommended for use in the assessment of the welfare of domestic fowl.

CHAPTER 8 Passive Avoidance

8.1. Introduction

In a typical conditioned suppression experiment, changes in operant response rate are recorded as a result of the onset of a conditioned stimulus (CS) which has previously been associated with an aversive event. When the CS is terminated, the subject receives the aversive event irrespective of its behaviour i.e. the subject *cannot* avoid the fright.[1] As there is no contingency between operant responding and delivery of the aversive stimulus, it is an example of pure classical conditioning.

Alternatively, a contingency between the operant response and the aversive stimulus can be arranged such that if the subject stops responding it *does* avoid the fright. As the subject only receives the fright if it continues to respond, the operant response is effectively punished. This purely instrumental, response-contingent fright technique has, therefore, become known as 'punishment'. This is a somewhat unfortunate choice of terminology given that, in general use, the term punishment has such negative connotations. The term 'passive avoidance' is a far more suitable term for this technique. It was first used by Mowrer (1960) when he argued that punishment and avoidance could be explained by a common set of principles (see Chapter 2). In a punishment experiment, the subject can avoid aversive stimulation by not doing something, i.e. it can avoid it passively. Conversely, shuttle and one-way avoidance can be called 'active avoidance' because the subject has to do something in order to avoid i.e. it can only avoid actively. Therefore, this chapter will use the term 'passive avoidance' to refer to this response-contingent fright

[1] The experiment described in Chapter 6 was not a typical conditioned suppression experiment in that the subject *could* avoid the fright by moving into the other compartment of the shuttle box. However, if the subject remained in the same compartment, it received the fright irrespective of whether or not it performed any (food reinforced) operant responses.

technique, although the term punishment will occasionally be used in a more general sense.

There are three basic methods of implementing a passive avoidance procedure. The simplest method is to switch from reinforcing the operant solely with food to reinforcing it solely with an aversive stimulus (e.g. Estes, 1944). The punishing stimulus simply replaces the food reward. However, this change results in the termination of food delivery. Consequently, the subject no longer has access to food, and it is effectively placed on an extinction schedule. Given that the extinction process itself results in a suppression of operant responding (Miller, 1951; Myers 1958), it is possible that operant suppression due to extinction will confound the measurement of the suppression resulting from punishment. The termination of food reinforcement can also lead to the rapid total suppression of the punished response (Azrin and Holz, 1961). Consequently, the technique would probably be unable to accurately discriminate between different levels of aversion, and, therefore, would not be suitable as a measure of aversion.

These problems can be overcome by continuing to deliver food reinforcement after the passive avoidance schedule is introduced. Perhaps the simplest means of implementing both food and aversive reinforcement is to superimpose the passive avoidance schedule on top of the food reinforcement schedule. For example, Azrin (1960) trained pigeons to peck at a plastic disc for a food reward on a variable interval 1 minute schedule. This schedule was then changed so that the bird received a brief electric shock after every response. This resulted in a decrease in the operant response rate, with the response rate being inversely proportional to the shock intensity. However, after continued exposure to both mild (30V for 30ms) and moderate (50V for 100ms) punishment, the response rate started to recover, suggesting that the subjects were habituating to the aversive stimulus. Responding during severe (100V for 30ms) and very severe (130V for 100ms) punishment showed no sign of recovery, with total response suppression with very severe punishment. The problem with this approach is that the subject can only get access to food by receiving shocks and as a result it has to pay a very high price (i.e. no food) in order to avoid. Although such a technique may allow a fairly accurate estimate to be made of the price an animal is prepared to pay (in terms of the amount of food it is prepared to forgo) in order to avoid, it is a very harsh schedule. Therefore, the technique has to be rejected as a measure of aversion on ethical grounds.

A more satisfactory approach is to give the animal some way of discriminating between responses which will be punished and those which will

result in food delivery, thus enabling the animal to avoid punishment but still receive food. One such method is the 'response-shift' technique. For example, Azrin and Holz (1966) describe an experiment using pigeons performing an operant response using two circular response keys. The subject could initially use either one or both keys to work for a food reward on a fixed ratio 25 schedule. This schedule was then changed such that one of the keys delivered an electric shock every time it was pecked. At shock intensities above 40V, the subjects quickly learnt to stop pecking the key which delivered shock, but continued to respond on the other key which gave the food reward.

An alternative to this third approach is to use a discriminative passive avoidance technique. This involves just one operant manipulandum, but uses a discriminative stimulus to signal when the punishment schedule is active. For example, Church, Wooten and Matthews (1970) trained rats to press a lever for food reward on a variable interval one minute schedule. A variable interval one minute punishment schedule was then superimposed on the food reinforcement schedule. This lasted three minutes, and was signalled by a white noise discriminative stimulus. After a number of these trials, the subjects learnt to suppress responding during the discriminative stimulus, therefore, avoiding further electric shocks. Another group of subjects received a similar treatment, except that shock occurred at the end of the white noise presentation irrespective of the rats' behaviour i.e. a conditioned suppression paradigm. For a given shock intensity, the degree of suppression recorded was greater under the passive avoidance paradigm than the conditioned suppression paradigm.

One of the recommendations given in Chapter 6 was the use of discriminative techniques in positively reinforced operant conditioning. This gives the experimenter greater control over when the subject performs the operant response. Given that the discriminative passive avoidance technique already includes discriminative stimuli, it could be modified to incorporate discrimination stimuli signalling both negative and positive reinforcement. The aim of the experiment described in this chapter was to investigate whether domestic fowl can learn such a discriminative passive avoidance task.

8.2. Materials and methods

The subjects were housed in specially built 'mini-battery' cages which were constructed from commercial battery cage components (Figure 8.1). Each 'mini-battery' comprised four single cages, each 0.30m wide, 0.50m deep, 0.40m high at the rear and 0.50m high at the front i.e. the cages had sloping floors. A food trough

ran along the front of the cages, and a nipple drinker was located at the back of each cage. The test cage was one of the middle two cages of the mini-battery, and was fitted with an operant panel. This panel occupied approximately half of the cage front, the other half being fitted with piece of 25mm mesh. This ensured that the subject could get access to food only through the operant panel.

The birds were housed in these cages for the duration of the experiment (which was ten days). This was to overcome the problem encountered with the discrete trial approach used in the conditioned suppression experiment.

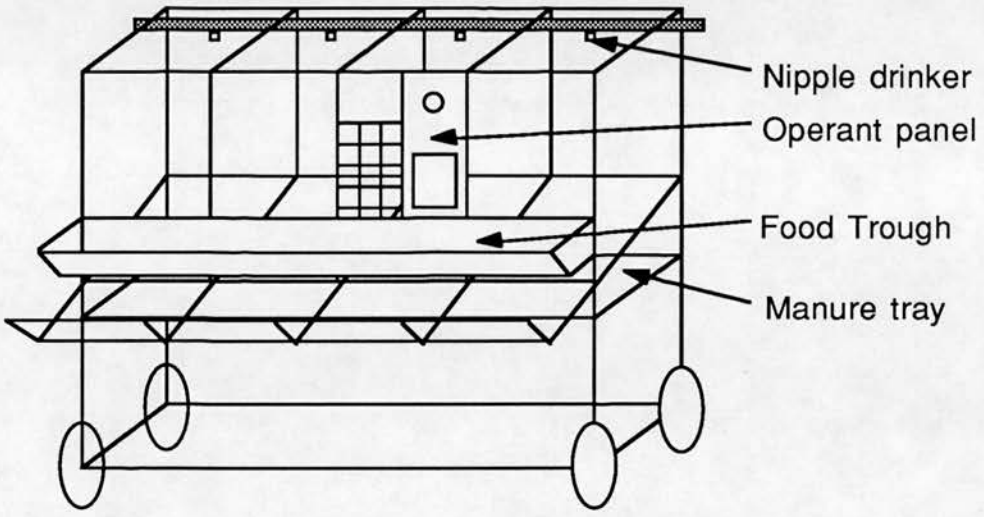

Figure 8.1. The 'mini-battery' cage used in the experiment.

The birds were first taught to perform an operant response, using the operant equipment described in Chapter 4. When the birds were first placed in the cage, the door in the operant panel was left open until the birds were feeding freely through it. The door was then closed, and a food pellet was stuck onto the operant key with clear adhesive tape. The operant system was then activated to deliver reinforcement (i.e. access to food for five seconds) on a fixed ratio one schedule i.e. every peck was reinforced. The majority of birds soon pecked at the food pellet and in so doing operated the operant key which resulted in the door opening and giving them access to food. After a number of such responses, the majority of subjects started to perform the operant response for food reinforcement. If after two days the subject had not started responding, the traditional hand shaping method was used. This involved reinforcing successive approximations of the operant response until the subject started to peck at the operant key. Once the bird had acquired the operant response, the operant schedule was slowly built up over a period of two days to variable ratio 12 i.e. the number of pecks required for each reinforcement was randomly varied between one and 23. A variable ratio schedule was used in

preference to the variable interval schedule used in the conditioned suppression experiment to overcome the problem of superstitious behaviour which was encountered in that experiment.

Over the next three days of the experiment, the subjects had to learn a discriminative operant task. The operant reinforcement schedule was only active for a total of 48 two minute sessions each day. The inter-session interval was randomly varied between five and 15 minutes. The start of each session was signalled by the illumination of the operant key and the presentation of one of two auditory stimuli, which lasted for the duration of the session. The two auditory stimuli were generated by a BBC Microcomputer which controlled the operant system, and the pitch envelope for these tones is shown in Figure 8.2. The tone presented for each session was pseudo-randomly varied such that during half of the sessions the high tone was presented and during the other half the low tone was presented[1].

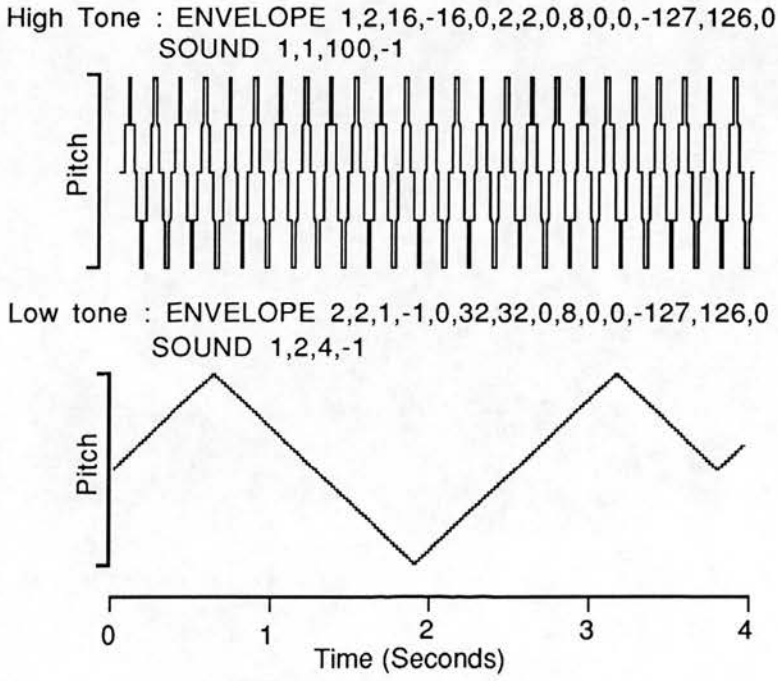

Figure 8.2. The pitch envelopes of the two discriminative stimulus tones along with the BBC BASIC commands to define and generate them.

The passive avoidance testing occurred on the last three days of the experiment. Subjects continued to receive 48 sessions per day. However, only one

[1] This used a random number routine which mimicked the withdrawal of numbered balls from a bag.

of the tones signalled food reinforcement (the 'food' tone). For the experimental treatment, if the bird responded and completed the schedule (i.e. performed the number of responses required for delivery of reinforcement) during the other tone (the 'dust' tone), the bird received a fright[1]. As in the one-way avoidance experiment, this involved the cage being dusted with a large feather duster. Given that there was an unavoidable delay between the bird performing the operant response which completed the ratio and the experimenter entering the room and frightening the bird, a classically conditioned link was used to ensure the bird associated the response with the presentation of the stimulus. This link was created by changing the nature of the discriminative stimulus from a variable to a fixed pitch tone immediately after the final operant response was performed. The fixed pitch tone lasted ten seconds, during which time the experimenter entered the room and dusted the cage. The experimental subjects could, therefore, avoid being frightened by suppressing operant responding during the 'dust' tone, but could continue to feed by responding during the 'food' tone. The reinforcement schedule is summarized in Figure 8.3.

It is possible that any response suppression during the 'dust' tone was due to the subjects realizing that they would not receive any food i.e. that the 'dust' tone signalled extinction. Alternatively, non-reinforcement itself has been shown to be aversive (Wagner, 1969) and may, therefore, have been the cause of response suppression instead of cage dusting. Consequently, a control group were subjected to a treatment which was identical to the experimental treatment except that they did not receive any frights. If a control subject completed the operant ratio during a 'dust' trial, the discriminative stimulus changed from a variable pitch tone to a fixed pitch tone, as in the experimental treatment. However, the experimenter did not frighten the bird, nor did it receive a food reinforcement.

As in the previous three experiments, the generality of the procedure was tested by using the S-line and T-line strains of hens described in Chapter 5. Five birds of each strain received the experimental treatment and five the control treatment, resulting in the familiar 2 x 2 design with four groups. Four test cages

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[1] Note that the food reinforcement schedule was not active during the 'dust' tone. This is believed to make the task easier to learn i.e. it is probably easier to learn that one tone gives food and the other a fright, as opposed to one food and the other food and a fright. This did, however, mean that the during the 'dust' tone the subjects were effectively placed on an extinction schedule, which, as discussed earlier, could confound the main treatment effect. However, the control subjects did not receive food reinforcement during the 'dust' tone either. Consequently, any differences between the control and experimental birds could be attributed solely to the effect of the aversive treatment.

were constructed and each was housed in a separate room (2.45m x 2.55m x 2.45m). This allowed four birds, one of each strain/treatment combination, to be tested simultaneously. One of the experimental birds in each group of four was monitored using a closed circuit television system, and general qualitative observations about these birds' behaviour were noted.

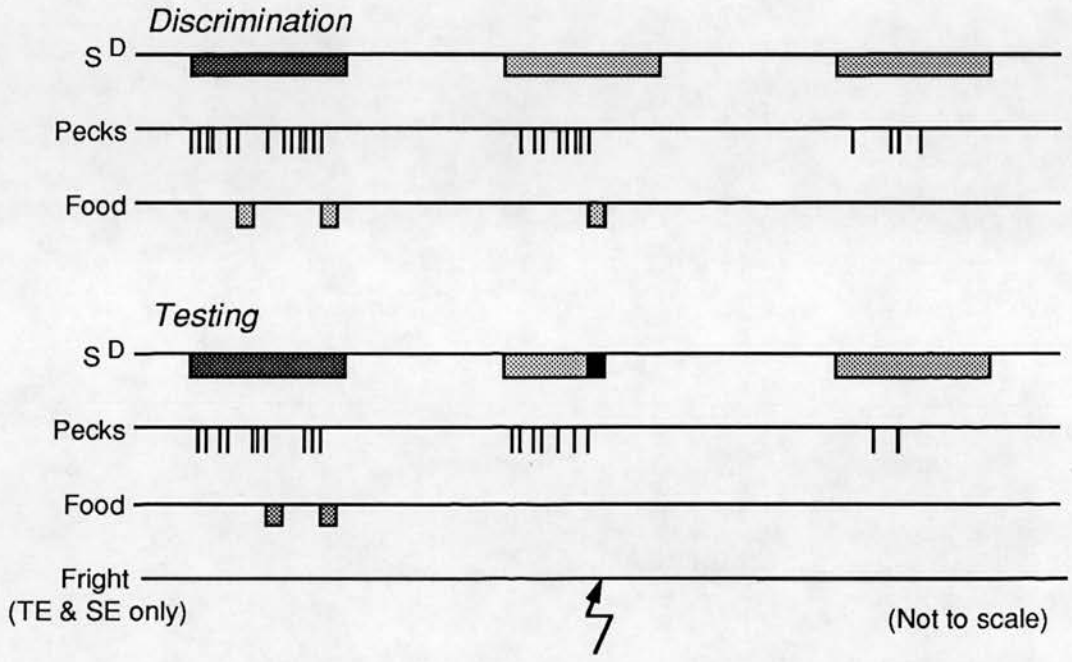

Figure 8.3. A summary of the reinforcement schedules used during the discrimination and testing stages. The two discriminative stimuli (S^D) are denoted by different shades of grey.

The actual tone (i.e. whether high or low) used for the 'food' and 'dust' discriminative stimuli (S^D) was pseudo-randomly varied such that half the subjects received the 'high' tone as the 'food' S^D and the low tone as the 'dust' S^D, and half received the low tone as the 'food' S^D and the high tone as the 'dust' S^D. This was so that the 'tone' effect was partitioned equally between both of the main effects (i.e. strain and treatment) i.e. food was associated with the high tone with three TE, two SE, two TC and three SC birds.

Four experimental subjects (TE16, TE17, SE16 and SE17) were implanted with heart rate transmitters. These transmitters are described in detail by Duncan and Filshie (1979). The implantation operation was performed under a general anaesthetic (30-60 mg Pentobarbitone Sodium [Sagatal™]) three days before the birds entered the experimental apparatus. The birds had, therefore, recovered from the effects of the operation before testing began. The operant control program recorded the number of heart beats occurring at ten second intervals.

8.3. Results

The raw data (the number of key pecks and reinforcements per trial) are given in full in Appendix IV. The data were analysed in terms of the number of trials on which the bird received reinforcement. Table 8.1 shows the number of food and dust reinforcements received by each bird on the last day of discrimination training and on each of the three test days. On the third day of testing, no experimental subject received more than one fright (out of a possible 24).

	Discr. day 3		Test day 1		Test day 2		Test day 3	
Bird	food	food	food	dust	food	dust	food	dust
TE16	20	20	9	3	5	1	12	1
TE17	13	15	10	3	8	1	9	0
TE18	18	15	3	5	14	5	2	0
TE19	20	20	9	7	13	2	15	0
TE20	19	17	7	6	10	1	5	1
SE16	14	13	18	5	18	3	24	0
SE17	11	12	2	2	1	1	6	0
SE18	7	9	4	5	3	2	7	1
SE19	14	15	3	5	0	0	0	0
SE20	18	14	4	1	6	1	0	1
TC16	22	13	19	17	24	21	19	18
TC17	20	20	23	21	24	24	22	21
TC18	18	14	11	12	21	21	23	16
TC19	14	13	22	21	21	21	21	22
TC20	18	19	22	22	24	24	19	20
SC16	11	10	8	12	12	7	20	13
SC17	23	21	2	1	10	13	23	21
SC18	9	12	0	0	5	3	14	10
SC19	17	22	18	19	20	17	21	19
SC20	23	24	12	10	22	23	24	24

Table 8.1. The number of food and dust reinforcements received by each subject on the last day of discrimination training and each of the three test days.

A regression analysis (Figure 8.4) on the number of food (*f*) and dust (*d*) reinforcements showed that the regression lines had intercepts near the origin. Consequently, the data could be analysed in form of the ratio *d/f*.

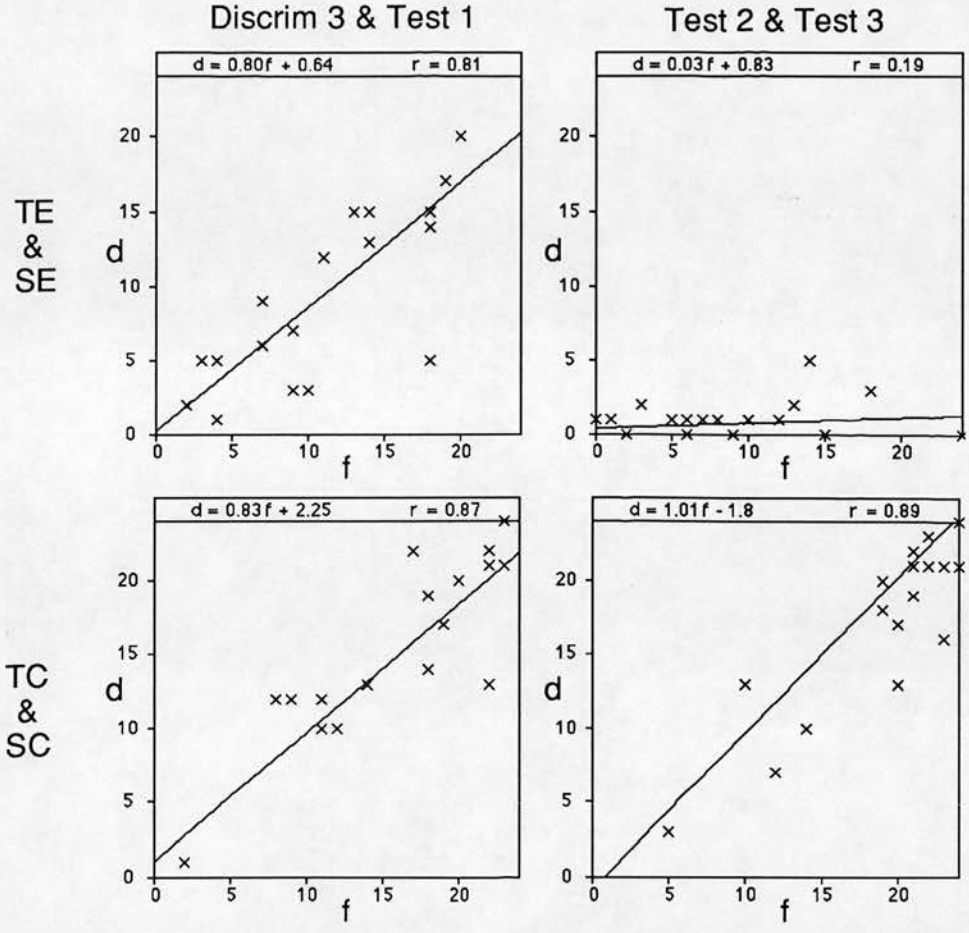

Figure 8.4. Regression analysis of the number of food reinforcements (f) against number of dust reinforcements (d). To isolate any treatment or learning effects, the data were split by treatment and day.

Given that the frequency distribution of ratio values is not often normal, a Box-Cox analysis of the ratios was performed. This analysis produces the optimum power transformation (lambda) which gives the data an approximately normal distribution (Box and Cox, 1964). The Box-Cox analysis showed the minimum deviation occurred at a value of lambda of 0.4. The ratio values were therefore raised to the power 0.4 before being analysed by an Analysis of Variance (Table 8.2). The ratio $(d/f)^{0.4}$ was significantly lower in the experimental group than the control group ($F_{1,12} = 31.97$, $p < 0.001$), showed a significant fall from the last discrimination learning day to the last test day ($F_{3,35} = 30.49$, $p < 0.001$) and showed a

significant interaction between the treatment and the day ($F_{3,35} = 25.69$, $p < 0.001$).

Source of variation	d.f.	s.s.	m.s.	F	p
Between subjects					
Strain	1	0.0189	0.0189	0.33	
Treatment	1	1.8342	1.8342	31.97	<0.001
Tone	1	0.0343	0.0343	0.60	
Strain.Treatment	1	0.0167	0.0167	0.29	
Strain.Tone	1	0.0018	0.0018	0.03	
Treatment.Tone	1	0.0003	0.0003	0.00	
Strain.Treatment.Tone	1	0.0005	0.0005	0.01	
Residual	12	0.6885	0.0574		
Within subjects					
Day	3	2.2588	0.7529	30.49	<0.001
Strain.Day	3	0.0578	0.0193	0.78	
Treatment.Day	3	1.9030	0.6343	25.69	<0.001
Day.Tone	3	0.0094	0.0031	0.13	
Strain.Treatment.Day	3	0.0975	0.0325	1.32	
Strain.Day.Tone	3	0.0275	0.0092	0.37	
Treatment.Day.Tone	3	0.0142	0.0047	0.19	
Residual	35(4)	0.8644	0.0247		
Total	75(4)	6.7518			

Table 8.2. Analysis of Variance results on the ratio of $(d/f)^{0.4}$. The ratio 0/0 was taken to be undefined and there were therefore 4 missing values.

The heart rate transmitter in bird TE17 failed to give a clear signal. The transmitters in birds TE16 and SE16 failed completely during the first day of testing. Although the transmitter in bird SE17 gave a clear signal throughout the experiment, it was decided to abandon attempts to record the heart rate. Consequently, what little data were collected were insufficient for a meaningful analysis. However, the signals recorded during the first frights received by TE16, SE16 and SE17 showed information relevant to the discussion and are, therefore shown in Figure 8.5.

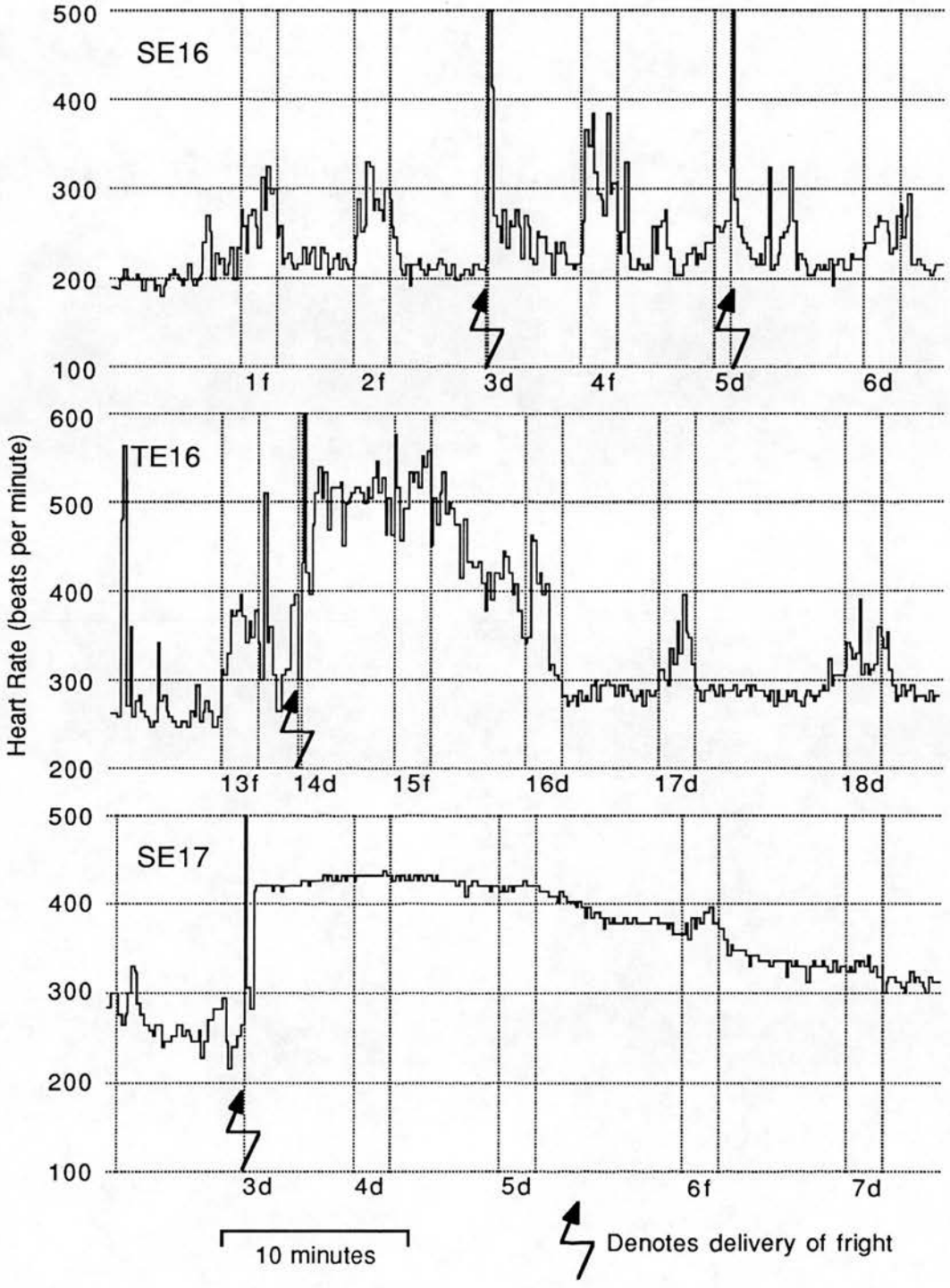

Figure 8.5. Plots of heart rate against time for the first fright received by three of the subjects (TE16, SE16 and SE17). The vertical dotted lines indicate the start and finish of S^D trials, the trial number and nature (i.e. food[f] or dust[d]) being given beneath each trial.

8.4. Discussion

Although the majority of the control subjects continued to respond during the 'dust' tone, even though they received no reinforcement, there were two exceptions. SC18 stopped responding altogether on the first day of testing. As the bird received no reinforcement whatsoever, there was no obvious reason for this; the bird just seemed to 'take a day off'. However, the bird started to respond again on the second test day, and received more reinforcements on the last day of testing than on the last day of discrimination learning. SC17 responded and received food reinforcement during the first two trials on the first day of testing. The third trial was a 'dust' trial, and the bird responded and completed the ratio, but, as this was during the test stage of the experiment, it received no food. It appears that the bird found this non-reinforcement aversive as it did not show any further responses for the rest of the first day. However, the bird resumed responding on the second test day and on the third day it received 23 'food' reinforcements and completed the schedule on 21 'dust' trials. This suggests that the bird did not find non-reinforcement very aversive. It is, however, possible that the control subjects found non-reinforcement during 'dust' trials frustrating and the operant responses recorded during those trials were due to a frustration effect (Amsel, 1958; Wagner, 1959).

8.4.1. Heart rate

The failure of the heart rate transmitters was a considerable disappointment. The problems were due to the physical stress they were exposed to when the birds showed frantic escape activity as they were frightened i.e. transmitter leads were broken and sutures holding the electrodes in position became loose. The one transmitter which survived probably did so because the bird in which it was implanted (SE17) received only three frights. This problem has implications for the use of such physiological recording in the future. Unless much more robust transmitters can be built and electrodes can be more securely attached to the subject, the reliable recording of heart rate in a free moving subject, before and after such aversive stimulation, will not be possible. Although criticized earlier, physiological measures have a very important role to play in the assessment of animal welfare. It is, therefore, of the utmost importance that the problems reported here are overcome.

8.4.2. Learning to avoid frights

The results clearly show that the experimental subjects quickly learnt to avoid being frightened by suppressing their operant responding during the 'dust' tone, hence the significant effects of treatment (i.e. the effect of the aversive stimulus) and day (i.e. the learning effect) and the significant treatment x day interaction (i.e. only the experimental birds learnt to suppress the operant response during the dust tone).

During the discrimination stage of the experiment, the birds soon learnt that only those responses performed during 'a tone' resulted in access to food. The nature of the tone did not seem to matter, as the birds did not appear to show any preference for either tone. This tone vs no-tone discrimination task should be quite easy to learn, as no matter how much the subject pecked during the intervals between trials it never got any food, but responding during either of the two tones did result in it being given access to food.

On the first test day, all of experimental the birds eventually performed enough responses during a 'dust' tone to receive a fright. There was no way that a bird could have associated the 'dust' tone with a fright before it received any frights. It was simply responding in order to get access to food, but received a unexpected fright instead. This raises an important question. Did the bird immediately associate the response with the fright i.e. did it 'realize' that the fright was contingent on the response? This is difficult to answer. The simple fact that some subjects did not respond during the trials which followed the fright does not necessarily mean that they had learnt the association. As described in Chapter 6, aversive stimulation itself often results in a general suppression of behaviour. The fact that a bird stopped responding could have been due to it showing a suppression of behaviour after it had received a fright. However, such suppression is unlikely to last for more that a few minutes, and the suppression of operant responding lasted much longer than this in many of the birds. For example, after SE20 had received its first fright (on trial 7 of the first day), it did not show any responses for the rest of that day. It is unlikely that the general suppression as a result of the fright would have lasted so long, and some other factor must have been responsible for this effect. This other factor could have been that the bird *did* immediately associate the response with the fright. Even if all of the birds did not immediately associate the response and the fright, the fact that half of the subjects received five or less frights over the duration of the experiment suggests that at least some of the birds did learn this association very quickly. Given that the experiment described in Chapter 7 showed that domestic fowl are very slow to

learn an active avoidance response, why did the passive avoidance subjects learnt the association between the response and the fright so quickly?

At first glance, the passive avoidance task appears very complicated when compared with the one-way avoidance task. All the bird had to do in the latter was to walk through a door-way when a warning stimulus came on. In contrast, the passive avoidance task involved operant responses, discriminative stimuli, conditioned links and reversal learning. However, although the passive avoidance task appears complicated when looked at as a whole, virtually all of the complicated components of the task were learnt by the subject before aversive testing began. The birds first learnt that pecking the key resulted in them being given access to food, and then that only pecks occurring during the presentation of a tone resulted in access to food. All of this occurred before the subjects received any aversive stimulation. (Consequently, from a theoretical point of view, it does not matter how long this stage takes [as long as all the subjects eventually learn the task] because there is no risk of the birds habituating to the aversive stimulus. From a practical point of view, however, it is obviously desirable for the subjects to learn as quickly as possible, in order to minimize the duration of the experiment.)

During testing, the birds had to learn that responding during one of the tones resulted in a fright. The rapid acquisition of this final stage was possibly a result of the birds being 'primed' for such learning by the preceding stages. The birds had only just learnt the associations between key pecking, food access and the discriminative tones. The fact that these associations had just recently been formed could have meant that when it was presented with a new paradigm (i.e. responses during one tone result in a fright) it could quickly acquire the new association.

If the bird did associate the response with the fright, or even if the bird only 'suspected' that there was an association between the two, the bird would have been placed in a dilemma the next time the S^D came on. If it did not respond, it had no way of receiving food. However, given that the last response resulted in a fright, if it did respond, it risked being frightened again. What should it do?

Whether or not the bird responded on the trial following the fright could have depended on how aversive the fright was compared to how hungry the bird was and its perception of the probability of receiving another fright if it did. If the bird did not respond it had to pay a price: foregoing the food it would have gained if it had done so. If it did respond it may have had to endure another fright. The bird would have had to weigh the potential benefit (i.e. food) against the possible adverse consequences (i.e. another fright) in making any 'decision'. If the bird did not find

the cage dusting very aversive, it may have chosen to take a risk and perform the response, in the expectation that it would get food. Alternatively, if the bird found cage dusting very aversive, it might not have been be prepared to run the risk of being frightened again, even though this meant that it would not get access to food. If the bird was not particularly hungry, it may have 'decided' to refrain from responding in the 'hope' that the situation might have changed in some way e.g. it might have been returned to its home cage. When, after some time this had not happened, the fact that the bird would be getting hungry may have resulted in it being prepared to take the risk and start to respond.

This would suggest that the more aversive the subject found the treatment, the less 'willing' it would have been to risk being frightened again. The bird would, therefore, have been prepared to wait longer, even though this meant it got hungrier, before risking pecking. Consequently, such a bird would have been expected to show more response suppression and therefore to receive fewer frights[1] in a given period of time (e.g. the duration of testing). Conversely, birds which were less frightened would not have been prepared to pay such a high price in order to avoid. They would, therefore, have started to respond sooner rather than later and would have shown less response suppression and consequently would have been expected to receive more frights in the given time period. Was this the case?

8.4.3. Fear of dusting and the number of frights received

Unfortunately, problems with the heart rate transmitters (discussed earlier) meant that very little heart rate data were recorded. However, the changes in heart rate as a result of the first fright were recorded in three birds. These three birds showed very different reactions to the feather duster. SE16 showed a minimal response to having its cage dusted. It made some escape attempts, but it did not appear to be very frightened. The fright only resulted in a small change in the bird's heart rate. It rose from 200 bpm to 250 bpm, but fell back to the normal baseline level after about five minutes. The fright did not result in much suppression of general behaviour and this bird started performing the operant response on the very next trial after the fright. This bird received a total of eight frights over the three test days.

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[1] The operant response is simply a 'means to an end'. It is the reinforcement which results from the performance of the response which 'matters' to the subject. Consequently, the data were analysed in terms of the number of frights (i.e. aversive reinforcements) received by the subject.

TE16 showed a fairly typical response (in relation to the rest of the birds tested) to having its cage dusted. The bird made attempts to escape and appeared to be moderately frightened. As a result of the fright the bird's heart rate rose from a baseline level of 300 bpm to over 450 bpm, returning to the normal baseline after approximately twelve minutes. This bird showed some general suppression of behaviour after the fright, and did not show any operant responses until the eleventh trial after the fright. This bird received a total of five frights over the three test days.

In contrast, SE17 showed an extreme response to being frightened. The bird made exaggerated escape attempts, throwing itself about the cage. Consequently, this bird looked to be very frightened by cage dusting. As a result of being frightened, the bird's heart rate rose from a baseline level of approximately 250 bpm to 430 bpm, and took about 30 minutes to return to normal. The bird remained motionless for quite a long period after the fright, and did not perform any operant responses until the twelfth trial after the fright. This bird received only three frights during the three days of testing.

These behavioural, physiological (i.e. heart rate) and psychological (i.e. number of frights received) variables are summarized in Figure 8.6. This clearly shows that the bird which was the most frightened by the first fright (as assessed by simple observation and physiological response) received the least number of frights, and the bird which was least frightened received the most frights. The results, therefore, support the idea that the more aversive the bird found the stimulus, the less willing it was to respond and so the fewer frights it received. However, given that this conclusion is based on the results from just three birds it must be considered to be tentative. The findings should be validated using a larger number of subjects once the problems with the heart rate transmitters are overcome.

Eventually all of the experimental subjects started to respond during a trial some time after the fright. It is very unlikely that a bird would have learnt the association between the S^D type and the type of reinforcement after just the one fright[1]. The birds therefore probably just re-started responding during 'a tone' and it would probably have been a matter of chance as to whether it was the food or the dust tone. The nature of this reinforcement would probably have had a significant

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[1] It is important to emphasize that the $S^D \rightarrow$fright association is not the same as the response→fright association. As discussed earlier, some birds may have learnt the response→fright association after only a few exposures to the aversive stimulus.

effect on the birds' perception of the experiment. If they received a fright, the association between the response and the fright would have been reinforced. Given that a bird had now received two frights in succession, the perceived probability of receiving yet another fright if it responded would have been increased. Consequently, the perceived risk would also have increased. This would have resulted in such a bird being less likely to respond on the next trial. If a bird received a number of frights in succession, it may well have come to perceive that the frights had completely replaced the food reinforcement and it might, therefore, have stopped responding altogether. If, however, food reinforcement followed the first fright, the perceived chances of receiving another fright would have been reduced. Such a bird may even have perceived that the fright as an isolated incident and that it would now be safe to continue responding. Either way, the likelihood is that this would have increased the probability of the bird responding on the next trial.

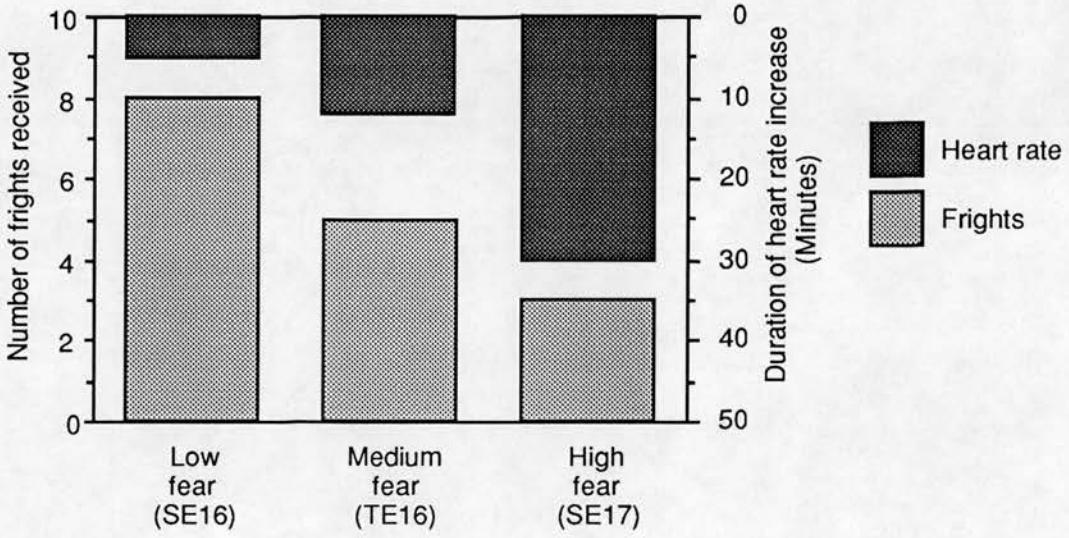

Figure 8.6. The relationship between the observed level of fear, the duration of the increase in heart rate in response to the first fright, and the total number of frights received during testing.

Similarly, subsequent dust reinforcements would have resulted in the perceived probability of a bird receiving a fright increasing, whereas subsequent food reinforcement would have resulted in this perceived probability decreasing. This would have continued until the birds eventually learnt that there was an association between the nature of the S^D and the type of reinforcement. Obviously, the birds would have needed to receive a sufficient number of both types of

reinforcement in order to learn the discriminative properties of the tone. If a bird received a number of consecutive dust trials, it would have had little opportunity to learn the food vs dust discrimination task before it stopped responding altogether. If, however, a bird had received a high proportion of food trials, interspersed with some frights, the conditions would have existed for it to learn, through repeated associations, that pecking during one tone resulted in food and pecking during the other resulted in a fright. This suggests that the sequence of reinforcements would have influenced whether or not a subject learnt to discriminate between the two tones. Was this the case?

8.4.4. Reinforcement sequence and discrimination learning

Before answering this question, it is important to define the conditions which demonstrated that a subject had learnt to discriminate between food and dust trials.

During the discrimination stage of the experiment, each subject worked for access to food on an average of 32.4 of the 48 trials. This suggests that, to have met their daily food intake requirement, the birds needed to receive reinforcement on this number of trials. Consequently, during the testing stage, subjects would have been expected to have worked for food on all 24 'food' trials, and even then this would have only provided three quarters of their daily food intake requirement. However, in practice, although the birds performed the operant response on an average of 32.4 discrimination trials, they did not feed on every trial. The birds appeared to find the operant response itself rewarding, and would perform the response even though they had no intention of feeding. Similarly, key pecking in pigeons is "hedonically loaded" (Toates, 1986), and pigeons will peck at a key even though this actually delays the delivery of reinforcement (Williams and Williams, 1969). Consequently, the birds could have gained sufficient food to meet their daily intake requirement from less than 32.4 trials. Also, by feeding more quickly, the birds could probably have met their intake requirement in fewer trials.

Ideally, the actual amount of food eaten by the birds would have been recorded during the experiment. Unfortunately, the food trough was both large and securely attached to the cage and did not facilitate the recording of food intakes. However, intakes recorded during the conditioned suppression experiment suggest that, when a bird is hungry (i.e. has been food deprived for 24 hours) it eats, on average, 2g in one five second reinforcement period. This is approximately 1.5% of the average daily food intake for a laying hen. Given that a bird could typically receive up to ten reinforcements in a two minute trial, this suggests that it could

meet its daily food intake requirement in approximately seven trials. Consequently, any subject which, on the last day of testing, received food on seven or more food trials, but received no frights could be said to have learnt the 'food' vs 'dust' discrimination. Three of the ten experimental subjects reached this criterion. If, however, the birds are allowed one 'mistake' i.e. they received no more than one fright on the last day, then half the experimental subjects could be said to have learnt the 'food' vs 'dust' discrimination.

Figure 8.7 shows the reinforcements given on the first day of testing for four experimental subjects, the best two (i.e. those receiving a considerable number of food rewards but no frights on the last test day, namely SE16 and TE19) and the worst two (i.e. those receiving very few food rewards on the last test day, namely SE19 and TE18) 'food' vs 'dust' discriminators. SE16 was the only bird to show total discrimination, receiving no frights on the last day of testing, but receiving food reinforcement on all 24 of the food trials. On the first day of testing, this bird received five frights, which is only slightly more than the average (4.2) for all the experimental subjects on that day. However, this bird received 18 food reinforcements on the first test day, considerably more than the average of 6.9. Figure 8.7 shows that SE16 generally received at least three food reinforcements between each fright. TE19 also learnt the 'food' vs 'dust' discrimination, receiving no frights but food on 15 of the food trials on the last day. This bird received six frights and nine food reinforcements on the first day. Although this bird received some consecutive frights, these blocks of consecutive frights were interspersed with a number of food reinforcements. Consequently, these two birds must have perceived the experiment as consisting of both food and aversive reinforcement. As they received a relatively large number of each, they had the opportunity to learn the discriminative properties of the S^D.

In contrast, SE19 and TE18 did not learn the 'food' vs 'dust' discrimination. SE19 received no food after the 23rd trial on the first day. With the exception of that one food reward, the bird received five consecutive frights on the first day. Similarly, with the exception of one food trial, TE18 received five consecutive frights on the first day. As a result, these birds probably perceived food reinforcement as being replaced with frights and, therefore, stopped performing the operant response.

These results demonstrate that the sequence of reinforcement can affect the learning of the discrimination task. The fact that the actual sequence of reinforcements that the bird received was random introduced an element into the learning procedure which acted to increase the variability of the final results. As

was demonstrated earlier, a subject receiving food reinforcements between frights was more likely to continue to respond, receiving more reinforcements. Therefore, until it learnt the food vs dust discrimination, it probably also received more frights. However, a bird which received a number of consecutive frights was more likely to give up responding altogether. Although two such subjects might have found cage dusting equally aversive, the one receiving the food reinforcements would have showed less response suppression (and, therefore, received more frights) than the one receiving just frights. Clearly, it would be beneficial if the random nature of the reinforcement could be eliminated.

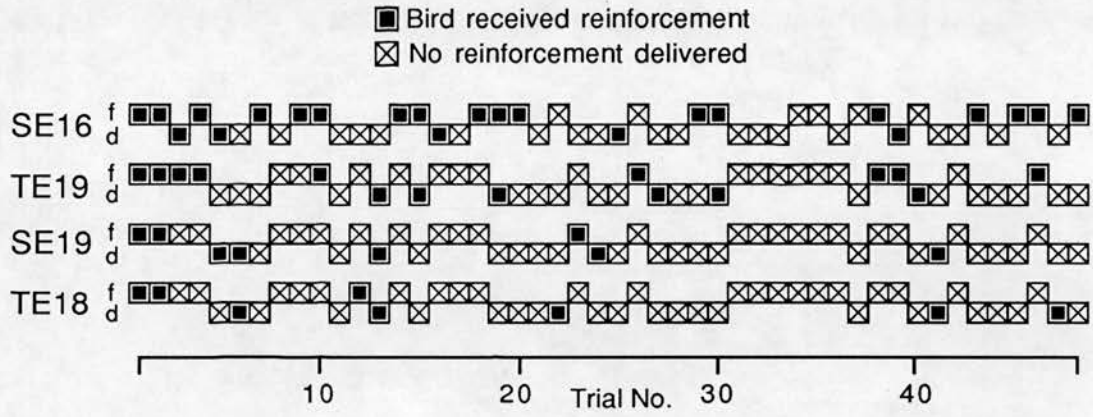

Figure 8.7. The order of reinforcements given on the first day of testing for two birds which learnt the discrimination task (SE16 & TE19) and two which did not (SE19 & TE18). Boxes above the centre line denote 'food' (f) trials and boxes below 'dust' (d) trials.

The randomness was, to some extent, produced in two ways. Firstly, the sequence of 'food' and 'dust' trials was created at random by the computer. This could be easily changed by the experimenter. However, whether or not the bird pecked on a given trial also introduced a random element which was beyond the control of the experimenter. That is, the experimenter had no way of knowing whether or not the bird would respond before the tone was actually presented. For example, the only way the experimenter could have ensured that the subject next received a food reinforcement would have been to continue presenting the 'food' S^D until the bird did respond. If a 'dust' S^D was presented and the bird did respond so that it completed the schedule, the bird would have had to have received a fright. However, the repeated presentation of just one of the S^D would then have made it impossible (or at least very difficult) to present the two S^Ds in a balanced way. This would have resulted in the subject receiving either more food or more dust

S^Ds, which could in itself have affected the subject's ability to learn the discrimination task.

The only way to overcome this problem would be to remove the 'food' vs 'dust' discrimination element. The procedure would then involve the presentation of just one type of S^D, which would simply indicate that the operant schedule was active. However, it would not indicate what type of reinforcement would be delivered. The experimenter could control the order of reinforcement delivery in such a way as to ensure that the results gave a more reliable indication of how aversive the animal found the treatment. The variability of the measure could, therefore, be reduced by presenting the same sequence of reinforcements to all subjects. The optimum order of presentation could, to some extent, be determined experimentally by using a variety of presentation patterns and observing which gave the highest degree of discrimination between different levels of aversion. The optimum presentation order would probably be based on an initially low frequency of frights. This would ensure that subjects which found the treatment very aversive did not stop responding immediately. The relative frequency of frights could be slowly increased until the birds stopped responding altogether i.e. they reached some criterion of a number of consecutive trials without reinforcement (Figure 8.8). The more trials it took to reach this criterion, the less aversive the subjects found the treatment. This non-discriminative passive avoidance technique could prove a very sensitive method of determining the aversiveness of a stimulus.

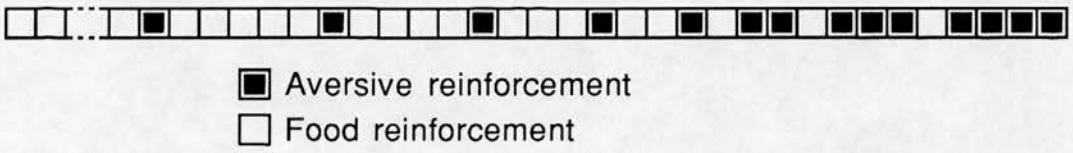

Figure 8.8. A possible sequence of reinforcement in which the probability of the subject receiving an aversive reinforcement increases with the number of reinforcements it receives.

However, these suggested changes result in a technique which no longer allows the subject to differentiate between food and aversive reinforcement. This approach was criticized in the introduction for being too harsh because the subject could not avoid aversive stimulation without foregoing food reinforcement. However, the fact that in a discriminative passive avoidance technique the subjects are given S^Ds which denote either food or aversive reinforcement does not necessarily mean that they *can* discriminate between the two. Indeed, discriminative passive avoidance is all about the subject having to learn this

discrimination task. Until the subject does learn to discriminate between 'food' and 'dust' trials, it is effectively receiving the non-discriminative procedure. Once the subject has learnt to discriminate between 'food' and 'dust', it should avoid further aversive stimulation and so there is little point in continuing testing the subject. If the non-discriminative procedure does yield a measure of aversion which has a smaller variance than the discriminative technique, significant differences between treatments could be detected with fewer experimental subjects. Consequently, the non-discriminative passive avoidance approach would mean fewer subjects would have to undergo the experimental treatment. The non-discriminative approach would, therefore, seem to be preferable to the discriminative approach and it warrants further investigation.

8.4.5. One-way vs passive avoidance

As Figure 8.9 shows, the birds in the passive avoidance experiment received significantly fewer exposures to the aversive stimulus than birds in the one-way avoidance experiment ($F_{1,18} = 23.5$, $p < 0.001$)[1]. Given that less exposure to the aversive stimulus is less likely to result in problems with habituation, passive avoidance is clearly a more appropriate measure of aversion than one-way avoidance.

Although active avoidance and passive avoidance have traditionally been viewed as two very different concepts, there are obvious similarities between the two (Mowrer, 1960). Active avoidance, as its name suggests, involves the subject actively avoiding an aversive stimulus. However, if a subject does not avoid it is *punished.* Passive avoidance, as its traditional name suggests, is involved with the punishment of behaviour. However, a 'punishment' subject can *avoid* aversive

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[1] Such a comparison is, statistically speaking, invalid because the analysis is based upon one variable i.e. the whole experimental paradigm. This one variable was, however, made up of a number of different variables i.e. warning stimulus type, duration and timing of the experiment etc. It is possible that there were significant but opposite effects within these variables which, when combined into the single variable, cancelled out. The results of this analysis must, therefore, be treated with caution. Ideally, this comparison should be performed in a single experiment. However, it is difficult to imagine an experiment which could directly compare two such different experimental techniques. Any design which did allow the two techniques to be compared directly would probably require considerable modifications to the experimental procedures. These modifications would probably compromise the ability of these techniques to discriminate between different levels of aversion. Consequently, although such a study could provide information of use to the learning theorists, the results would be of little use to those interested in developing practical measures of aversion.

stimulation by not performing the punished response. This suggests one possible reason why subjects can learn an passive avoidance task more readily than an active avoidance task. In a passive avoidance task, any behaviour other than the response which is punished results in the subject avoiding the aversive stimulus. Only one response is punished. Therefore, *any* change in the subject's behaviour will result in it avoiding another fright. In contrast, in an active avoidance situation (e.g. one-way avoidance) there is only one effective avoidance response (e.g. walking through a doorway). Any behaviour which is incompatible with this response (i.e. virtually all of the rest of the subject's behavioural repertoire) is punished. An active avoidance subject must, therefore, change its behaviour in a very specific way in order to avoid. The chances are that it will take the subject quite some time before it 'discovers' exactly which one response is an effective avoidance response. This could well account for why an active avoidance response is less readily acquired than a passive avoidance response.

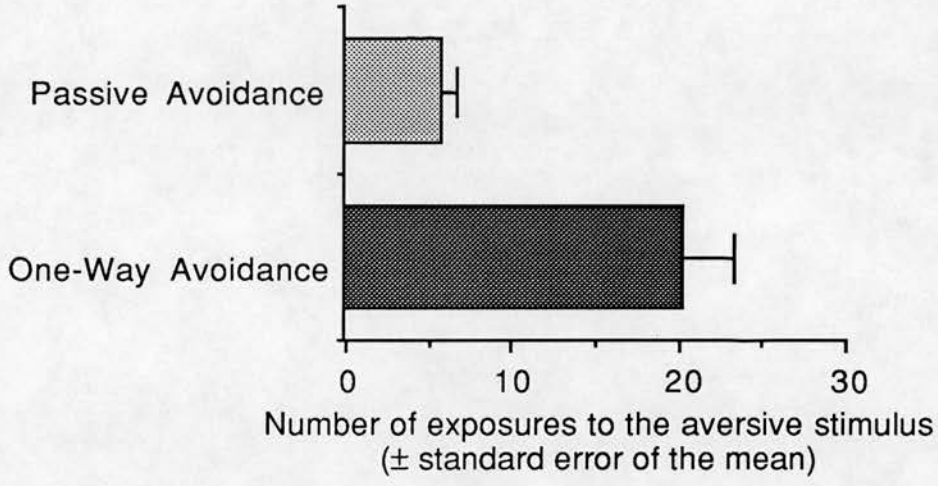

Figure 8.9. Histogram showing the mean number of frights received by passive avoidance subjects over the first 48 'dust' trials compared to the number received by the one-way avoidance subjects.

8.4.6. Conditioned suppression vs passive avoidance

Although conditioned suppression and passive avoidance appear to be very similar techniques (i.e. they both involve suppression of an operant response as a result of aversive stimulation), the two are based on fundamentally different concepts. Conditioned suppression is an example of classical conditioning. The aversive stimulus (the US) follows the CS regardless of the subject's behaviour. Although the procedure often involves operant conditioning, the operant response

is associated with the delivery of some positive reinforcer and is not associated with the US. Indeed, operant behaviour is only used as a 'baseline' behaviour because it is relatively stable and can, to some extent, be controlled by the experimenter. The suppressive effects of CS onset on other behaviour can be recorded. For example, Bouton and Bolles (1980) demonstrated that both the licking of a sucrose solution and spontaneous activity were suppressed by the onset of an auditory CS paired with an electric shock. In contrast, passive avoidance is an example of operant conditioning. The behaviour of the subject *does* determine if the aversive stimulus is given i.e. if the subject performs a particular response it is punished. If the subject does not perform this response, it can avoid aversive stimulation. Again, the reliable nature of operant behaviour makes it a suitable response to be punished. Just as other behaviour can be used as a baseline in conditioned suppression, other behaviour can also be punished. However, as was described in Chapter 3, some behaviour is not suppressed when punished. For example, responses which are elicited by aversive stimulation (e.g. aggression, certain defence reactions) appear to be facilitated by punishment (Melvin and Anson, 1969; Walters and Glazer, 1971; Melvin and Ervey, 1973).

Some learning theorists prefer not to draw such a sharp distinction between classical and operant conditioning (e.g. Dickinson, 1980). However, one of the most consistent findings of studies investigating both conditioned suppression and passive avoidance is that response contingent shock results in greater response suppression than does non-contingent shock (Estes, 1944; Church, 1963; Church, Wooten and Matthews, 1970). This is not particularly surprising when one considers the nature of the response suppression under each paradigm. Suppression as a result of the presentation of a CS appears to be due to some emotional response to the CS. It is, therefore, a very indirect effect due to the formation of a mental state, which results in a very general suppression of behaviour. The suppression resulting from a response being punished is far more direct. It is just the one response which is punished, and once the subject learns to suppress this response it can avoid subsequent aversive stimulation. Therefore, given that the aversive stimulus has a more direct effect on the suppression of the response, passive avoidance would be expected to show better discrimination between different levels of aversion. Indeed, this appears to be the case. Hake and Azrin (1965) demonstrated that a passive avoidance procedure allowed greater discrimination between different levels of shock intensity than conditioned suppression. Passive avoidance procedures also produce response suppression with treatments which are not aversive enough to produce conditioned

suppression. For example, Riccio and Thach (1966) demonstrated that cage rotation at 20 rpm was not an effective US in establishing conditioned suppression in rats, but that it was effective in punishing a food reinforced operant.

Passive avoidance, almost by definition, involves less exposure to the aversive stimulus than conditioned suppression. In a conditioned suppression experiment the subject receives a fright in *every* trial. Under a passive avoidance paradigm, the subject only receives a fright if it performs the response which is being punished. Once the subject has learnt which response is being punished, it can avoid all subsequent frights by simply not performing the response. In a given number of trials, a subject under a passive avoidance paradigm would therefore receive fewer (or at least no more) frights than a subject being tested under a conditioned suppression paradigm. Clearly, given that passive avoidance results in less exposure to the aversive stimulus, it is less likely to encounter problems with habituation.

The fact that most passive avoidance experiments (this one included) involve the punishment of a response which has previously been associated with food may appear to be highly stressful to the subject. However, Hunt and Brady (1955) found that a passive avoidance procedure resulted in less defecation and urination, and in less general behavioural suppression. Given that these are typical signs of stress, it therefore appears that passive avoidance is generally less stressful than conditioned suppression. This is probably due to the fact that passive avoidance subjects can avoid aversive stimulation, and therefore can actually control its presentation. Conditioned suppression subjects cannot avoid the US, and consequently have no control over it. This leads to another question; what is the relationship between control that an animal has over its environment and the stress it experiences?

Brady (1958) found that monkeys receiving Sidman avoidance training (described in Chapter 2) developed more gastric ulcers than animals which received the same pattern of electric shocks but which could not avoid them (known as 'yolked' controls). Brady suggested that this was due to stress resulting from the animal's ability to control the delivery of shock, in a similar way to which stress and anxiety in business executives causes them to develop similar gastro-intestinal disorders. However, as Brady (1958) himself pointed out, the secretion of acid (which caused the development of the ulcers) only occurred after each test session, in the six hour interval between avoidance sessions. Also, Weiss (1968) pointed out that Brady had not selected the 'executive' and control subjects at random i.e. the animal which learnt the avoidance response more

quickly was chosen as the Sidman subject. When the subjects were assigned to experimental and control groups at random (Weiss, 1968), Brady's (1958) findings were reversed: the yolked control subjects developed more and more severe ulcers than the Sidman subjects, and the controls showed other symptoms associated with stress e.g. reduced growth rate and increased defecation. It is now generally accepted that having control is less stressful a lack of control (e.g. Weipkema, 1988).

Passive avoidance is, therefore, more likely to be able to differentiate between different levels of aversion, is less likely to result in habituation problems and is a less stressful procedure than conditioned suppression. Consequently, passive avoidance appears to be a far more suitable measure of aversion than conditioned suppression. However, the conditioned suppression paradigm does have one benefit. Given that the US is presented regardless of the subjects behaviour, it is possible to test a large group of subjects simultaneously. In contrast, passive avoidance depends very much on the behaviour of the individual, and consequently only one subject can be tested at a time. This is not much of a problem for the psychologist, who usually only tests individual subjects anyway, but it could be a problem if the technique is to be used to assess the aversiveness of husbandry procedures under commercial conditions. A typical example might be in a experiment to investigate the aversive effects of transport in a transport simulator. In some respects, this is more suited to a conditioned suppression experiment. A number of birds could be given operant panels, and one CS could be given to all the subjects to warn them that the treatment (a simulation of the movement, vibration and noise caused by transport in a lorry) is about to begin. Such a situation is not, however, suited to passive avoidance, as only one subject could be tested at a time. If an attempt was made to test more than one bird, it is almost certain that on at least one trial, one subject would perform the punished response but another would not. The one that did respond would therefore have to be punished. However, the act of punishing this bird (i.e. turning the simulator on) would also 'punish' the other bird for a response it did not perform.

The fact that data from more individuals could be collected under a conditioned suppression paradigm could result in the technique showing significant differences between treatments in a shorter duration experiment than if a passive avoidance technique was used. This would be particularly important if the duration of access to the test facilities was limited (as is the case with certain transport simulators). However, given that the conditioned suppression technique is

generally more stressful than a passive avoidance technique (discussed earlier) it should only be used when no other option is available.

In addition, the operant-Pavlovian distinction between conditioned suppression and passive avoidance can be used to assess how *control* over aversive stimulation effects the level of aversion. The importance of the relationship between control and stress was emphasized earlier, and, in some respects, the two techniques ask two different questions. A passive avoidance experiment essentially asks "what are you prepared to pay in order to *avoid* a particular aversive stimulus?", whereas conditioned suppression asks "how do you feel about being exposed to an aversive stimulus which you *cannot control?*". This distinction could provide the basis for investigations into the effect of control on the subjective feelings of aversion experienced by domestic animals.

8.5. Conclusion

Although there are likely to be certain situations where a conditioned suppression technique could make better use of the available resources, passive avoidance is generally more suitable for use in welfare research. The technique was readily learnt by the majority of subjects tested and, therefore, meets both of the first two criteria laid down in Chapter 3. However, before the technique can be recommended for use in welfare research it must be shown to be empirically valid i.e. to discriminate between different levels of aversion. This is discussed further in the final chapter.

CHAPTER 9 General Discussion

9.1. Introduction

The principal conclusion to be drawn from the experiments described in the previous four chapters is that active avoidance techniques cannot be recommended for use in the assessment of animal welfare. Although conditioned suppression may be useful in certain experimental conditions, passive avoidance techniques appear to be the most reliable measures of aversion. However, one important question remains unanswered; can passive avoidance discriminate between different levels of aversion i.e. is it empirically valid?

9.2. Empirical validity

The problems associated with testing the empirical validity of any psychological measure were discussed in Chapter 3. The conclusion from that discussion was that empirical validity should be tested by seeing if the technique can discriminate between treatments *believed* to differ in their aversiveness, looking for correlations between the aversiveness of the treatment and physiological and behavioural indices of stress.

It was hoped to include such an experiment in this study. However, the four experiments reported in this thesis were all that could be accomplished within the three year study period. Indeed, the inordinate length of time needed to perform such studies has implications for their general practicality, and this problem is discussed later. Consequently, the empirical validation of passive avoidance as a measure of aversion in domestic fowl will have to wait for another day. However, results from this study and the aversion learning literature provide some evidence as to the empirical validity of the four techniques. All of the previous studies which have investigated the effects of exposure to different levels of an aversive stimulus have used electric shock as the aversive stimulus. As discussed in Chapter 3,

electric shock is a very unnatural stimulus, and caution should be used when evaluating its effects. However, the assumption that high intensity or long duration shock is more aversive than short duration or low intensity shock "seems reasonable" (Rushen, 1986c), and can at least give an indication of the empirical validity of the various techniques.

The relationship between shock intensity or duration and shuttle avoidance responding is not very clear. In dogs, increasing the shock intensity results in a greater number of subjects acquiring the avoidance response, however, this effect is reversed at the highest shock intensities (Brush, 1957). Similarly, rats generally fail to acquire a shuttle avoidance response at high shock intensities (Moyer and Korn, 1964; Johnson and Church, 1965; Theios, Lynch and Lowe, 1966; McAllister, McAllister and Douglas, 1971), resulting in an inverse relationship between shock intensity and shuttle avoidance responding. At lower shock intensities, the acquisition of an active avoidance response appears to be an "all-or-nothing" effect, with a sudden switch from very low avoidance response rates to very high response rates (when the majority of shocks are avoided) at a certain shock intensity (de Souza, de Moraes and Todorov, 1984). Consequently, such techniques cannot differentiate between different levels of aversion.

There are contradictory reports of the possible relationship between shock intensity and one-way avoidance responding. Theios *et al* (1966) found no relationship between the two, McAllister *et al* (1971) found that the shortest one-way avoidance response latencies occurred at the highest shock intensities, and Moyer and Korn (1966) found that shortest response latencies were associated with both the highest and the lowest shock intensities. Such contradictory results suggest that one-way avoidance cannot differentiate between different levels of aversion.

In contrast, one of the most consistent findings of passive avoidance studies is the direct relationship between shock intensity or duration and the degree of response suppression, in both pigeons (Azrin, 1960; Azrin, Holz and Hake, 1963; Hake and Azrin, 1965; Azrin and Holz, 1966; Church, 1969; Rachlin and Herrnstein, 1969) and rats (Appel, 1964; Boe and Church, 1967; Church, Raymond and Beauchamp, 1967). Study of the "trade-off" between the intensity of the shock received if the animal continues to respond and the food it looses if it suppresses operant responding (e.g. de Villiers, 1980) could be used to 'titrate' positive against negative reinforcement, and so provide an accurate measure of the 'price' an animal is prepared to pay in order to avoid certain stimuli (Rushen, 1986c). Similarly, conditioned suppression studies have shown a direct relationship

between shock intensity and duration and the degree of response suppression (Annau and Kamin, 1961; Hendry and Van Toller, 1965; Davis, 1968; Riess and Farrar, 1973; Hymowitz, 1981). However, passive avoidance does appear to be more sensitive to the effects of shock intensity or duration than does conditioned suppression (Hake and Azrin, 1965; Church, Wooten and Matthews, 1970). Subjects can show complete suppression of operant responding at high intensity or long duration electric shock in conditioned suppression experiments (Annau and Kamin, 1961; Riess and Farrar, 1973) and in passive avoidance studies (Azrin, 1960; Azrin and Holz, 1961). As discussed in Chapter 6, complete response suppression and complete conditioned suppression can reduce the ability of the technique to discriminate between different levels of aversion. However, it is possible that the problems of complete response suppression can be overcome, and Chapters 6 and 8 suggest how this might be achieved.

These findings clearly indicate that passive avoidance and conditioned suppression are generally empirically valid, whereas shuttle and one-way avoidance are not. In a recent review of the empirical validity of psychological measures of aversion, Rushen (1986c) reached a similar conclusion. He stated that "some of the procedures of aversive conditioning, namely suppression of appetitive feeding behaviour by punishment or aversive classical conditioning, reliably result in behavioural changes ... that contain information about the intensity and duration of the electric shock used in the conditioning" and that "the applied ethologist can therefore use these techniques with some confidence to assess the aversiveness of animal husbandry operations and handling treatments" (Rushen, 1986c).

The results from the passive avoidance experiment reported in Chapter 8 also showed evidence that suggests passive avoidance is empirically valid. Although the experiment only incorporated one type of aversive stimulus, the behavioural and physiological observations suggested that different subjects experienced different levels of aversion when they were cage dusted. As Figure 8.6 showed, the subject which was the most frightened received the least number of frights and the subject which was the least frightened received the most frights. This suggests that the number of frights the subject received was inversely proportional to the level of aversion the subject experienced. However, as this proof is based on only three frights received by three different birds, there is a probability of 0.17 that it is due to chance[1]. This conclusion must, therefore, be

[1] There are 6 different orders for three categories (i.e. if the three categories were A, B and C, then the six possible orders are ABC, ACB, BAC, BCA, CAB,

considered to be tentative and the technique must still be validated in a multi-treatment experiment.

It, therefore, appears that the two techniques which this study has shown to be learnt quickly by the majority of subjects tested (i.e. passive avoidance and conditioned suppression) are empirically valid, whereas the two techniques which were not learnt either quickly or by the majority of subjects (i.e. one-way and shuttle avoidance) are not empirically valid. Is this just a fortunate coincidence? I would suggest that it probably is not just coincidence. The fact that a number of subjects either fail to learn or are very slow to learn a given avoidance task is likely to increase the variance of any measure of their performance. Any treatment effects could be 'lost' within this inherent variance. Consequently, the technique would be less likely to be able to discriminate between different levels of aversion. Also, repeated exposure to the aversive stimulus as a result of the subject's failure to perform the avoidance response may result in the subject habituating to the aversive stimulus. This would probably confound the measurement of aversion, which would again result in the technique being less likely to discriminate between different levels of aversion.

9.3. General Problems

The problems associated with the specific techniques have already been discussed. However, there are a number of problems which apply either to the work covered in this thesis as a whole, or to aversion learning techniques in general.

9.3.1. Experience of the experimenter

It is clear that passive avoidance is the most promising technique for assessing animal welfare. However, passive avoidance was also the last technique to be tested. Indeed, there is a distinct relationship between the order in which the techniques were evaluated and their relative success. The first, shuttle avoidance, was a comparative failure. Although the second, conditioned suppression, was more successful than shuttle avoidance, there were still a considerable number of problems. The third, one-way avoidance, was moderately successful, although the subjects did receive a lot of frights before they learnt the avoidance response. The last, passive avoidance, was generally a success.

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and CBA), therefore the probability of one of these orders (e.g. ABC) occurring by chance is 1 out of 6 i.e. 0.17.

To some extent, this was only to be expected. I learnt a lot from the earlier failures, and no doubt the knowledge that I had gained designing and performing the first three experiments contributed to the success of the last. It is, therefore, possible that, if I were to use this knowledge to redesign the first three experiments, they would yield results as good as, if not even better than, the passive avoidance experiment. However, I honestly believe that this would *not* be the case. The impression I got from observing the birds in the passive avoidance experiment was that they quickly 'realized' what was required in order to avoid. In contrast, the birds in the shuttle box did not appear to have perceived what was required for successful avoidance, and, more importantly, I cannot think of any changes in the experimental paradigm which would significantly improve avoidance performance in either the shuttle box or the one-way apparatus. I do, however, believe that the implementation of the changes to the conditioned suppression experiment which were outlined in the discussion of that technique would result in a significant improvement. However, I still believe that response-contingent reinforcement would be superior to non-contingent reinforcement, given that the former includes an avoidance contingency. In addition, the principal conclusion of this study is supported by the literature. Generally, active avoidance techniques are not very readily acquired by any animal or bird species. In contrast, passive avoidance and conditioned suppression generally are learnt quickly, with operant aversive reinforcement being superior to classical aversive conditioning. Therefore, I do not believe that the knowledge I gained in performing the earlier experiments invalidates the main conclusion i.e. that passive avoidance techniques are the most reliable measures of aversion.

9.3.2. Effects of experimental parameters

All of the techniques investigated in this study have a number of parameters associated with them, such as inter-trial interval, warning stimulus or S^D duration, operant reinforcement schedule, the number of trials per session, the nature of the warning stimulus etc. Many of the studies reported in the aversion learning literature have found that these parameters can significantly influence the extent to which a given task is learnt by a subject. Given that conditioned suppression has been the most widely used aversion learning technique (Bouton and Bolles, 1980), the majority of the research into the effects of experimental parameters have involved conditioned suppression. For example, the intensity of the CS (Kamin and Schaub, 1963), the duration of the CS (Libby, 1951), the CS duration relative to CS off-time (Stein, Sidman and Brady, 1958), reinforcement frequency (Lyon, 1963)

and reinforcement schedule (Lyon, 1964) can all affect the degree of conditioned suppression. Similarly, experimental parameters associated with active avoidance techniques can influence the acquisition of the avoidance response. For example, the nature of the warning stimulus (e.g. visual versus auditory) can affect the acquisition of a lever-press avoidance response in rats (Jacobs and LoLordo, 1977).

Consequently, it is possible that had the shuttle avoidance experiment used different experimental parameters (e.g. a longer inter-trial interval, or splitting testing over a number of sessions), all of the subjects would have acquired the avoidance response. In contrast, changes in the parameters associated with the passive avoidance technique may have resulted in the subjects failing to avoid the aversive stimulus. However, as mentioned earlier, the results reported in this thesis are the same as those found in the majority of aversion learning studies. i.e. that generally, animals find it difficult to learn active avoidance tasks but find tasks involving response suppression as a result of aversive stimulation comparatively easy to acquire. Also, as I stated earlier, I do not believe that changes in the parameters associated with the shuttle avoidance or one-way avoidance techniques would result in a significant improvement in the either the number of subjects acquiring or the number of trials taken by the subjects to acquire the avoidance response. However, substantial modifications to the passive avoidance procedure could impair its ability to discriminate between different levels of aversion. Consequently, the influence of experimental parameters should be considered when adapting any of these techniques for use in future studies.

9.3.3. Other aversion learning techniques

This investigation has looked at only four aversion learning techniques. However, there are a number of other aversion learning techniques, principally active avoidance techniques and it is possible that one of these may be a more reliable measure of aversion. A variety of locomotor and non-locomotor active avoidance techniques have been developed. Theoretically, any behaviour could be chosen as the avoidance response[1]. Traditionally, however, psychologists have used those responses which can be readily recorded i.e. lever or bar pressing in mammals and key-pecking in pigeons. However, both pigeons (Hoffman and Flesher, 1959; Hineline and Rachlin, 1969; Schwartz, 1973) and rats (Biederman *et*

[1] However, as pointed out earlier, the fact that an experimenter chooses to reinforce a response does not necessarily mean that the animal is able to acquire the response as an avoidance response.

al, 1964; D'Amato and Schiff, 1964; Riess, 1971) find such avoidance responses very difficult to acquire and require extensive training and elaborate shaping. Even then, a large number of subjects fail to acquire the response at all (Bolles, 1970). With extensive training, pigeons can learn to depress a treadle or lever in order to avoid an electric shock (Foree and LoLordo, 1970; Smith and Keller, 1970). Rats can learn to avoid an electric shock by running in a wheel more readily than rearing up on the hind legs (Bolles, 1969) and can learn to avoid by remaining still more readily than moving about (Brener and Goesling, 1970).

Unsignalled (Sidman) avoidance was first demonstrated by Sidman (1953), and was described in Chapter 2. This involved the subject performing a free-operant avoidance response in order to avoid an unsignalled aversive stimulus. The reinforcement schedule was such that each response delayed the delivery of an electric shock for a given interval, which was 20 seconds in Sidman's (1953) experiment. Therefore, the subject could avoid the shock by responding at least once every 20 seconds. However, such an avoidance response is not very readily acquired (Foree and LoLordo, 1970).

Given that all of these alternative techniques require extensive training involving a considerable number of exposures to the aversive stimulus, the problem of habituation could confound the measurement of aversion (as discussed in Chapter 3). Consequently, such techniques are not suitable as measures of aversion.

A 'true' one-way avoidance task (as opposed to the technique used in Chapter 7) involves the subject moving from a location where aversive stimulation can occur to a location where it never occurs, and such a task is very readily learnt (Page, 1955; Theios and Dunaway, 1964; Beecroft, 1967). In fact, the task is acquired so readily, often after just one trial (e.g. Maatsch, 1959), that the technique would not allow much discrimination between different levels of aversion i.e. learning would be an 'all-or-none' event, with no intermediate rates of acquisition of the response. Consequently, the technique would not be suitable for use as a measure of aversion.

Locomotor passive avoidance involves punishing an animal for running down a runway to obtain food. It has been shown that the reduction in speed of this response is a positive monotonic function of the intensity of the electric shock (Miller, 1959; Karsh, 1963). The technique has already been used to assess the aversiveness of electro-immobilization in sheep (Rushen, 1986b). Consequently, locomotor passive avoidance looks to be a promising technique, and warrants further investigation.

9.3.4. Repeatability of the measure

Unlike physiological techniques, aversion learning studies do not give an absolute measure. Indeed, as was pointed out in Chapter 3, the fact that aversion is an intervening variable means that it can never be measured on a continuous scale, and can only be measured on an ordinal scale. Consequently, there cannot be any units of aversion. Although variables, such as the number of frights received by a subject, could be used to rank the treatments investigated in one study, such variables are also affected by the parameters associated with each technique (as discussed earlier). Consequently, unless two research groups used identical experimental procedures, it would be very difficult to compare the results from two different groups.

This problem could be overcome to some extent if a standard set of aversive stimuli could be defined. However, it is difficult to conceive exactly which stimuli could be used to form a set of standards. Different intensities or durations of electric shock would be the most obvious choice. However, there are a number of problems associated with the use of electric shock (discussed earlier) and its use in welfare research would also be questionable on ethical grounds. An alternative would be to use particular husbandry procedures themselves as standards. In the case of laying hens, this could include exposure to cage dusting, operation of the manure scrapers or the approach of a human. Clearly, if such procedures were to act as 'standard aversive stimuli', they would have to be performed in a controlled and well defined manner. Mechanical operations, such as the operation of the manure scraper could be very precisely defined (e.g. the size of the scraper unit, the speed at which it travels, its distance beneath the bird etc.) and such procedures could be quite easily replicated by other research groups. However, procedures which involve a human operator could not be defined so precisely. For example, although the brush used in cage dusting could be defined (e.g. colour, bristle length etc.), the manner with which it is used by the operator would be considerably more difficult to define. However, the mechanical operation of cage dusting could, to some extent, be automated by the use of robotics. This would allow the path and speed of brush to be defined in such a way as it could be replicated by another group. Although the procedure would no longer be a true representation of the commercial practice of cage dusting, the procedure could, however, be used as one of the standard aversive stimuli.

If the use of aversion learning techniques in the assessment of animal welfare becomes more widespread, only when such a set of standards are agreed

amongst all of the research groups undertaking such studies, will different groups be able to compare their results.

9.3.5. Practical considerations

Given that the main aim of this study was to determine which aversion learning techniques are suitable for the assessment of animal welfare, the practical application of these techniques must also be considered. Ideally, the measurement of the aversiveness of particular husbandry procedures should be performed in the environment in which these procedures are practiced. This would ensure that all of the factors associated with a given husbandry procedure (e.g. the effects of other conspecifics, the physical nature of cages, the cage level etc.) would be taken into account in any measurement of the aversiveness of the procedure. In the case of the laying hen, the birds' principal environment is the battery cage, although investigation of the procedures associated with pre-slaughter transport and handling would involve a number of different environments (although the birds would probably be confined to a transportation crate during exposure to the majority of transport related procedures). The implementation of any of the techniques which have been investigated in this study would require at least some changes to the bird's physical environment (i.e. the battery cage or transportation crate). However, if these changes were substantial, the measurement of the aversiveness of the procedures would not occur under true commercial conditions and the recorded levels of aversion could differ significantly from the actual levels experienced in commercial systems. Consequently, any changes necessitated by the implementation of the technique should be minimal.

The greatest changes would be associated with the use of the one-way avoidance apparatus. It is difficult to conceive how a standard battery cage could be modified so as to incorporate the necessary function of this complex piece of apparatus. This technique could only be used by moving the whole apparatus into a commercial poultry house. However, this would remove the influence of neighbouring birds, and could not be used to investigate any cage level effects. (Jones [1985] has shown that cage level can influence the fearfulness of domestic fowl.)

Implementation of a shuttle avoidance technique would involve considerably fewer changes. The necessary function of the shuttle box could probably be achieved by placing a doorway between two adjacent battery cages, with the two cages acting as the two compartments of the standard shuttle box. (Indeed, it may only be necessary to put a strip of tape across the centre of the two cages to give

the cage the functional properties of a shuttle box [P.Duncan, reported in Bolles, 1975]). Similarly, implementation of both the conditioned suppression and passive avoidance techniques would require only minimal interference with the bird's physical environment. This would simply involve the cage front being replaced with an operant panel such that the bird could get access to food only through the doorway in the operant panel. Commercial battery cages or transportation crates usually have more than one bird per cage or crate. However, all of the techniques investigated in this study have used a single subject. The fact that operant conditioning involves reinforcing a response performed by an individual subject means that all of the avoidance techniques (i.e. one-way, shuttle and passive avoidance) are restricted to testing one subject at a time. Although it is theoretically possible to test one subject within a group of conspecifics, in practice the presence of other conspecifics would probably interfere with the conditioning procedure (e.g. social interactions could prevent the subject from performing an avoidance response). This is a serious limitation to the practical implementation of operant aversion learning (i.e. avoidance) techniques which is impossible to overcome.

However, it is possible that a group of birds could be tested together using conditioned suppression. The group could be given access to one or more operant panels and could then be given a CS to signal that an particular husbandry procedure is about to be performed. Consequently, the suppressive effects of the CS could be recorded in the subjects performing the operant response during this period. Unfortunately, there are a number of problems associated with operant group feeding, the commonest of which is where one subject performs the operant response and another group member 'steals' its reward (e.g. McBride and Craig, 1985). Consequently, the accurate measurement of conditioned suppression may only be possible using individually caged subjects.

Perhaps the greatest constraint on the practical application of these techniques is the inordinate length of time taken to perform aversion learning experiments. Each of the experiments described in this thesis took between four and six months to complete. To establish a reliable estimate of the distribution of aversion levels within the population of animals being studied, large groups of animals will need to be tested. Given that there are a number of potentially aversive husbandry procedures (indeed, all procedures should be considered to be potentially aversive), the whole process will involve testing hundreds, possibly thousands of subjects. Consequently, a systematic study of all of the husbandry procedures associated with a particular production method would involve a

considerable amount of effort. Unless the problem of the repeatabilty of such measures (discussed earlier) can be overcome, the entire study would have to be performed by one research group. Such a study would probably take a number of years to complete and would clearly involve a considerable economic commitment. Indeed, I believe that the relatively high cost of using an aversion learning approach will probably determine, above all else, if it is actually used in the assessment of animal welfare.

9.3.6. Nature of the aversive stimulus

This study has used two aversive stimuli i.e. the rapidly inflating balloon and cage dusting with a feather duster. The rapidly inflating balloon is a looming stimulus which may be aversive because it suddenly fills the animal's field of vision and is interpreted as something rushing towards the animal very quickly and therefore something which could be dangerous. The sudden appearance of the feather duster may also be perceived as a looming stimulus or it may be frightening because it has the characteristics of a predator (Duncan, 1985). In any event, they are aversive because they are frightening. However, fear is not the only cause of aversion. The state of frustration is also believed to be aversive (Duncan and Wood-Gush, 1972b). Can these techniques be used to assess the aversiveness of frustrating situations?

The success of conditioned suppression and passive avoidance were due, to some extent, to the generally suppressive effects of frightening stimuli. However, frustrating stimuli can often have an accelerative effect on behaviour (i.e. act to increase the probability of the behaviour occurring). For example, Duncan and Wood-Gush (1972b) showed that the thwarting of the feeding behaviour in domestic fowl resulted in displacement preening, stereotyped pacing and, in some instances, escape movements. Frustration also increases aggressive behaviour in the domestic fowl (Duncan and Wood-Gush, 1971).

Clearly, a CS indicating that a potentially frustrating situation was about to occur could result in the subject showing a higher response rate than before the CS came on, even if the subject found frustration aversive. In the passive avoidance experiment the control groups did not receive any food reinforcement during the 'dust' tone. Such non-reinforcement is a typical example of a frustrating situation, although none of the birds made any attempt to avoid it by suppressing operant responding during the 'dust' tone. Given that frustration appears to have an accelerative effect, it is entirely possible that subjects could be trained to perform an active response to avoid frustrating situations. So, whilst techniques such as

one-way avoidance and shuttle avoidance are not suitable measures of fear related aversion, these techniques might be appropriate for measuring the aversiveness of frustration. Indeed, Wood-Gush and Guiton (1967) found that domestic fowl will attempt to avoid (in a general sense) frustrating situations. Pigeons can learn to peck a key in order to turn off a light on another key which signalled that food would not be delivered (Terrace, 1971; Rilling, Kramer and Richards, 1973). Given that frustration is believed to be detrimental to an animal's welfare (Duncan and Wood-Gush, 1972b) this approach warrants further investigation.

The inflating balloon and exposure to cage dusting were also very short duration stimuli, lasting at the most a few seconds. However, there are a number of relatively long term stressors which animals may find aversive, such as close confinement (e.g. battery caged hens, sows in stalls or tethers, veal calves in crates) or long term social isolation (e.g. veal calves). It is clearly impossible to attempt to use aversion learning to measure how aversive such long term stress might be. These stressors are essentially 'one-off', and cannot be repeatedly associated with either an operant avoidance response or a classically conditioned stimulus. The stress that these procedures cause can only be assessed using physiological and behavioural techniques.

Clearly, the aversion learning techniques are not *general* measures of aversion. Their use is largely restricted to relatively short duration, frightening stimuli. However, many husbandry practices fall within this category. Consequently, such techniques can be used to investigate a substantial number of the potentially aversive stimuli to which domestic animals are exposed.

9.3.7. Learning, cognition and suffering

Even if all the practical problems associated with the use of aversion learning techniques can be overcome, there still remains one insurmountable problem. This was raised in Chapter 1 and is that, as a mental state, aversion *cannot* be measured. Indeed, these techniques do not even tell us if animals *experience* the state of aversion. The simple fact that an animal *avoids* certain stimuli does not tell us if that animal experiences a mental state of aversion towards these stimuli. It is possible that the animal is showing a simple reaction to the noxious stimulus, in a similar way to which a computer control system 'reacts' when certain events occur.

The fact that the animal *learns* to avoid such stimulation in the future does not prove that it experiences a mental state of aversion either. Pearce (1987) suggested that the Cephalization Index, K, (i.e. the ratio $E/P^{2/3.2}$, where E is the average brain weight and P is the average body weight) of an animal species is

related to the 'intelligence' of the animal. For example, man has the highest K value of 0.89, followed by dolphins (0.64), chimpanzees (0.30), dogs (0.14), wild pigs (0.12) and rats (0.05). However, there is very little relationship between the Cephalization Index of an animal species and learning ability of that species (Pearce, 1987). For example, Warren (1965) reported that goldfish, domestic chickens, cats, horses and rhesus monkeys showed no difference in the rate at which they learnt to approach one of two stimuli for a reward. Bees can learn to discriminate between different colours in just two trials (Menzel and Erber, 1978), whereas pigeons, rats, raccoons and rabbits need at least 18 trials to learn a comparable discrimination task (Angermeier, 1984). A computer control system can be made 'artificially intelligent' so that it can formulate rules which would allow the system to take steps to avoid the occurrence of undesired events in the future. Very few people would argue that the computer would suffer if it were to be prevented from 'avoiding' the undesired event. Therefore, it does not necessarily follow that just because an animal learns to avoid certain stimuli that exposure to these stimuli 'means' anything (in a cognitive sense) to the animal involved.

This is, however, largely a philosophical problem. It is not even possible to determine if fellow human beings experience the same emotions as oneself. One can only assume that because other people act in a similar way to oneself, that they must also experience similar emotions. Accepting that fellow human beings feel these emotions, it is possible that other animals may do so as well, but we simply cannot tell. The problem then becomes an ethical issue. Most people, quite naturally, believe that other humans do experience the same, or at least very similar, feelings as themselves. Generally, people respect the feelings of others humans, and avoid actions which might cause others to suffer. Given that animals may experience emotions similar to our own, why do we not make similar efforts to avoid causing them any suffering?

One argument put forward by those who defend intensive farming methods is the fact that domestic animals have poor cognitive abilities in comparison to man. Consequently, it is argued, that their propensity to experience suffering is also less than man's. However, this need not be the case. Indeed, I suggest that reduced cognitive ability could well result in a *greater* propensity to suffer. The relationship between prediction, control and stress has already been discussed. Man's high cognitive ability allows us to comprehend and understand much of the world around us, and this understanding helps us control our daily lives. As a result, we generally do not live in fear for our lives. In comparison, the domestic hen in a battery cage may not comprehend many of the events which occur in its life and it

can do very little to control any of them. Consequently, the bird may genuinely be living in perpetual fear for its life, with every husbandry operation being a potentially lethal threat. Consequently, the fact that a hen avoids certain stimuli could, therefore, mean that exposure to these stimuli does 'mean' a great deal to the animal and any feelings of aversion they experience could be far greater than those experienced by human beings.

There is simply no way that we can ever know for certain just what 'aversion' means to a hen (or any other animal for that matter). It is, therefore, necessary to make one or two assumptions which cannot be based on scientific evidence. I would like to propose one such assumption. That is that *if an animal avoids a stimulus, it finds that stimulus aversive and that the greater the price the animal is prepared to pay in order to avoid, the more aversive the stimulus.* (This is not a new idea. As discussed in Chapter 1, Dawkins (1983) proposed assessing animal welfare by investigating the price animals are prepared to pay either to gain access to or avoid certain situations.) Of course, it does not necessarily follow that if the animal does not avoid a stimulus that it does not find that stimulus aversive. For example, an animal may engage in a fight to defend its territory. Although some individuals may actually enjoy fighting, most probably find it aversive, but they do not avoid such encounters. In this case, the price that the animal is being asked to pay in order to avoid is too high, i.e. the animal stands to lose its territory if it does not fight. In this situation, the animal perceives an aversive confrontation as the lesser of two evils, and consequently does not avoid it.

Also, as was demonstrated in the shuttle avoidance experiment, animals may adopt a different avoidance strategy to the one the experimenter chooses to reinforce, e.g. freezing instead of moving into the adjacent compartment in a shuttle box. Consequently, the simple fact that an animal fails to 'avoid' a stimulus does not necessarily mean that it does not find that stimulus aversive. However, as long as the experimenter chooses to reinforce an avoidance response which the animal itself perceives as being effective (e.g. a true one-way avoidance or a passive avoidance response), then the animal should be able to acquire the response if it finds the stimulus aversive.

Therefore, as long as the cost of avoidance is not too great and the experimenter gives the animal an opportunity to perform an effective avoidance response, I believe that we can expect animals to avoid situations which they find aversive.

9.4. Conclusion

It is clear that the aversion learning techniques are not going to provide any simple solutions to the problem of assessing animal welfare. The problems discussed in this and earlier chapters raise an important question; are these techniques worth the effort?

I hope that this thesis has shown that the psychological techniques can overcome many of the criticisms of behavioural and physiological techniques when used to assess animal welfare (discussed in Chapter 1). The results from the experiments reported in this thesis demonstrate that exposure to an inflating balloon or a feather duster can support various forms of learning, and this suggests that domestic hens find these stimuli aversive. Of the techniques which this study investigated, passive avoidance appears to be the most promising for use in the assessment of animal welfare. Although results from the passive avoidance experiment suggest that this particular technique can differentiate between different levels of aversion, these results must be considered to be tentative. Consequently, the study has not demonstrated that any of these techniques are reliable *measures* of aversion. However, I hope that the study has made an important first step, and that resources and effort can now be concentrated on showing that passive avoidance is empirically valid i.e. that it can differentiate between different levels of aversion. If the empirical validity of passive avoidance is established, the technique can then be used to determine how aversive domestic fowl find commercial husbandry practices.

As stated in Chapter 1, animal welfare is about how animals feel. Given that aversion learning techniques can give us some insight into what, if anything, animals might feel, I believe that such techniques have a vital role to play in the future of animal welfare research.

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Appendix I : An operant control program

The following listing is a complete operant control program for running a single operant panel. A full description of the program is given in Chapter 3. The program listing does not include line numbers, but could be typed in after entering the AUTO command in BBC BASIC.

```
REM   A Simple FR/VR/FI/VI Operant Control Program
REM           by Steven Mark Rutter, March 1989
CLS
PROCinit
PRINT
PRINT "Operant Control Program V1.0"
PRINT
IF fixed THEN PRINT "Fixed "; ELSE PRINT "Variable ";
IF ratio THEN PRINT "Ratio "; ELSE PRINT "Interval ";
PRINT; value; " reinforcement."
PRINT "Press f0 when door closed to stop the program."
PROCon
WAIT
PROCfile
PRINT "Finished."
END

DEF PROCinit
 REM ****** assign input/output channels ******
 key         = 0  : REM key switch
 upper_end   = 1  : REM upper motor end switch
 lower_end   = 2  : REM lower motor end switch
 light       = 3  : REM key light
 motor_power = 4  : REM motor power
 motor_dir   = 5  : REM motor direction
 timer       = 0  : REM food reward / interval timer

 REM ****** assign reinforcement variables ******
```

```
 ratio = TRUE      : REM ratio or interval schedule?
 fixed = FALSE     : REM fixed or variable schedule?
 value = 5         : REM ratio/interval (in secs) value
 sec_reward = 5    : REM duration of food reward in secs
 min_int = 7       : REM minimum inter-peck interval
 key_count = 0     : REM number of key pecks
 reward_count = 0  : REM number of reinforcements
 open = FALSE      : REM is the door open?
 prev_peck = 0     : REM time of last response

 REM ****** assign data storage variables ******
 DIM buffer 3      : REM reserve 3 bytes to store a record
 pointer = 0       : REM next free store location pointer
 good_key = 0      : REM event code for a good key
 bad_key  = 1      : REM event code for a bad key
 reward   = 2      : REM event code for a reward
 buffer_address$ = STR$~buffer
ENDPROC

DEF PROCon
 |(SWITCH key, ON) PROCkey_peck
 |(f0) PROCoff
 TIME = 0
 IF ratio THEN PROCset_ratio ELSE PROCset_interval
ENDPROC

DEF PROCoff
 IF NOT open THEN KILL ALL
ENDPROC

DEF PROCkey_peck
 IF ((TIME-prev_peck) < min_int) THEN ENDPROC
 prev_peck = TIME
 IF (SWITCH light = OFF) THEN PROCbad_key : ENDPROC
 PROCsave( good_key )
 PRINT "Key peck at TIME = "; TIME
 key_count = key_count + 1
 IF ratio THEN PROCratio ELSE PROCinterval
ENDPROC

DEF PROCbad_key
 PROCsave( bad_key )
ENDPROC

DEF PROCratio
 IF key_count >= reward_count THEN PROCopen
 PRINT; reward_count - key_count; " pecks left."
ENDPROC

DEF PROCset_ratio
 reward_count = key_count + FNincrement(value)
ENDPROC
```

```
DEF PROCinterval
 IF interval_over THEN PROCopen
ENDPROC

DEF PROCset_interval
 interval_over = FALSE
 |(TIMER timer, FNincrement(value) * 100) PROCint_over
ENDPROC

DEF PROCint_over
 interval_over = TRUE
 PRINT"Interval over; next peck rewarded."
ENDPROC

DEF FNincrement(inc)
 LOCAL r
 IF fixed THEN r = inc ELSE r = RND(2 * (inc-1)) + 1
= r

DEF PROCopen
 SWITCH OFF light
 |(SWITCH upper_end, ON) PROCstop_open
 SWITCH ON motor_dir
 SWITCH ON motor_power
 PROCsave(reward)
 PRINT "Reinforcement at TIME = "; TIME
 open = TRUE
ENDPROC

DEF PROCstop_open
 SWITCH OFF motor_power
 SWITCH OFF motor_direction
 |(TIMER timer, sec_reward * 100) PROCclose
ENDPROC

DEF PROCclose
 |(SWITCH lower_end, ON) PROCstop_close
 SWITCH ON motor_power
ENDPROC

DEF PROCstop_close
 SWITCH OFF motor_power
 IF ratio THEN PROCset_ratio ELSE PROCset_interval
 open = FALSE
ENDPROC

DEF PROCsave(event)
 time = TIME DIV 10
 buffer ? 0 = time MOD &100
 buffer ? 1 = (time DIV &100) MOD 100
 buffer ? 2 = (event * 32) + (time DIV &10000) MOD 4
```

```
 pointer$ = STR$~pointer
 OSCLI("srwrite " + buffer_address$ + " +3 " + pointer$)
 pointer = pointer + 3
ENDPROC

DEF PROCfile
 INPUT "Enter filename " filename$
 pointer$ = STR$~ pointer
 OSCLI("srsave " + filename$ + " 0 " + pointer$)
ENDPROC
```

Appendix II : A heart rate recording routine

The following 6502 assembly language routine was executed whenever an event occurred. The routine first checked to see if the event was the analogue to digital conversion complete event. If not, the event was probably a 'Spider™' event, and control passed to the 'Spider™' event routine. Otherwise, the routine read the result of the conversion and checked whether it was above the threshold (which was stored as an eight bit integer in memory location &0070). If not, any previous peak was 'over', so the peak flag (which was stored in the lowest bit of memory location &0071) was set to false. Otherwise if it was a peak, and the previous reading was not over the threshold, the highest line on the user-port was set high (this line was reset each time the routine was executed). This signal could be monitored along with the ECG pattern on an oscilloscope, and therefore facilitated a simple check on the accuracy with which the computer detected heart beats. The peak count (held as an eight bit integer in memory location &0072) was incremented (as long as it had not reached the point of overflow, i.e 255 beats) and the peak flag was set to true. The routine then returned control to the main program after restoring the accumulator and the processor status flag. The main program read the number of beats every ten seconds, after which the beat count (memory location &0072) was reset.

```
.event              \ by Steven Mark Rutter, August 1988
   php              \ save processor status
   pha              \ save accumulator (i.e. event type)
   cmp #3
   bne other        \ event not adc - let Spider try it
   lda &FE60        \ get user-port status
   and #&7F         \ and set top bit to low
   sta &FE60        \ to terminate a 'peak' signal
   lda &FEC1        \ read adc value (top eight bits only)
   cmp &70
   bmi null         \ branch to null if under threshold
   lda &71
```

```
   cmp #0
   bne exit          \ branch to exit if last reading a peak
.peak
   lda &FE60         \ get the user-port status
   ora #&80          \   and set the top bit high
   sta &FE60         \   to signal a peak
   lda &72
   cmp #&FF
   beq exit          \ branch if counter reached overflow
   clc
   adc #1            \ else increment counter
   sta &72
   lda #1            \   and set peak flag
   sta &71
.exit                \ general exit, so
   pla               \   restore the accumulator
   plp               \   restore the processor status
   rts               \   and exit
.null                \ the ADC was less than threshold, so
   lda #0            \   reset peak flag
   sta &71
   pla               \   restore the accumulator
   plp               \   restore the processor status
   rts               \   and exit
.other               \ the event wasn't an ADC event, so
   pla               \   restore accumulator
   plp               \   restore processor status
   jmp &FF30         \   jump to spider event routine
```

Appendix III : Conditioned suppression results

The following tables give the number of operant responses recorded in the minute before CS onset (column b); the number of operant responses recorded whilst the CS was on (column d); and, whether or not the bird showed an avoidance response on that trail (column a; 0 = no avoidance, 1 = avoidance) for each of the five birds in each of the four groups. The first 12 trials were 'test' trials - all subjects received exposure to the inflating balloon. The last 12 trials were extinction trials - all subjects received only the warning stimulus.

	TE2			TE5			TE8			TE9			TE10		
Trial	b	d	a	b	d	a	b	d	a	b	d	a	b	d	a
1	16	0	0	9	0	0	12	0	1	16	0	1	35	0	1
2	6	0	1	6	0	1	1	0	1	6	1	0	7	0	1
3	4	0	1	0	0	1	0	0	1	2	0	0	12	0	0
4	21	0	0	6	0	1	21	0	0	0	0	0	13	0	1
5	22	0	1	0	0	0	0	0	1	0	0	0	2	0	1
6	10	0	1	0	0	1	0	0	1	0	0	1	0	0	1
7	17	0	1	5	0	1	9	0	1	10	0	0	22	0	1
8	19	0	1	3	0	1	1	0	1	8	0	1	1	0	0
9	12	0	1	0	0	1	0	0	0	0	0	1	0	0	1
10	30	0	1	6	0	1	2	0	1	6	0	1	26	0	1
11	28	0	1	5	0	1	0	0	1	0	0	0	1	0	1
12	18	0	0	0	0	1	0	0	1	0	0	1	0	0	1
13	16	0	1	8	7	0	13	1	0	0	0	0	10	4	1
14	20	0	0	0	0	1	1	0	1	0	0	0	13	0	1
15	19	0	1	0	0	0	0	0	1	0	0	0	0	0	0
16	27	0	1	10	7	0	14	1	0	8	0	0	25	2	1
17	35	0	1	2	0	1	12	1	0	0	0	0	24	4	1
18	22	0	1	0	0	1	5	1	0	0	0	0	0	0	1
19	34	24	0	9	14	0	16	0	1	0	0	0	1	0	1
20	27	0	1	17	13	0	14	3	0	0	0	0	1	0	1
21	12	0	1	11	4	0	0	0	0	0	0	0	0	0	1
22	16	0	1	17	9	0	14	1	0	0	0	0	9	0	1
23	21	16	0	17	4	0	5	0	0	0	0	0	11	8	0
24	30	29	0	11	3	0	2	0	1	0	0	0	1	0	1

	SE1			SE3			SE4			SE6			SE7		
Trial	b	d	a	b	d	a	b	d	a	b	d	a	b	d	a
1	7	4	0	14	10	0	9	1	0	18	9	0	2	0	1
2	3	0	1	11	12	0	0	0	0	3	0	0	0	0	1
3	7	0	1	2	0	0	0	0	0	1	0	0	1	0	1
4	10	0	1	6	0	0	0	0	1	0	0	0	2	0	1
5	2	0	1	0	0	0	0	0	0	0	0	0	3	0	1
6	0	0	1	0	0	1	0	0	0	0	0	0	7	0	1
7	12	0	1	0	0	0	0	0	0	1	0	1	0	0	0
8	13	0	1	0	0	0	0	0	1	0	0	1	5	0	0
9	1	0	1	0	0	0	0	0	0	0	0	0	14	0	1
10	17	0	1	10	4	0	0	0	0	0	0	0	1	0	1
11	33	6	0	26	14	0	0	0	0	0	0	0	2	0	0
12	3	0	1	0	0	0	0	0	1	0	0	0	0	0	1
13	1	1	1	20	9	0	0	0	0	9	0	0	8	0	0
14	7	0	0	24	5	0	0	0	0	0	0	1	7	0	1
15	2	0	1	0	0	0	0	0	0	0	0	1	11	0	0
16	12	3	1	18	7	0	0	0	0	5	0	1	17	0	1
17	3	0	1	64	0	1	2	0	0	0	0	0	7	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0
19	17	5	1	21	5	1	0	0	0	11	0	0	24	20	0
20	31	6	0	64	4	0	0	0	0	0	0	1	4	0	0
21	1	3	1	0	0	0	0	0	0	0	0	0	5	0	0
22	18	13	0	18	8	0	9	0	0	0	0	1	36	2	0
23	1	4	0	1	0	0	3	0	1	0	0	1	0	0	1
24	4	4	1	5	0	1	0	0	0	0	0	0	20	1	0

	TC1			TC3			TC4			TC6			TC9		
Trial	b	d	a	b	d	a	b	d	a	b	d	a	b	d	a
1	14	0	0	16	7	0	5	0	1	7	0	0	0	0	0
2	3	0	0	0	0	0	0	0	0	1	0	0	2	0	0
3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	15	3	0	0	0	1	25	2	0	19	4	0
5	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1
6	0	0	1	0	0	0	0	0	1	1	0	1	0	0	1
7	11	0	0	0	1	0	1	0	1	4	0	1	0	0	0
8	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
10	0	0	0	28	8	0	13	0	0	43	10	0	14	4	0
11	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
12	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
13	0	0	0	15	14	0	2	6	0	42	7	0	13	6	0
14	0	0	0	1	0	0	8	5	0	40	3	0	0	0	1
15	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0
16	0	0	0	20	18	0	8	1	1	29	52	0	26	28	0
17	0	0	0	23	15	0	7	2	0	18	2	0	1	0	0
18	0	0	0	4	0	0	0	0	0	6	0	0	0	0	0
19	6	0	0	28	14	0	10	10	0	36	11	0	13	11	0
20	0	0	0	25	16	0	5	5	0	33	17	0	0	1	0
21	0	0	0	0	0	0	6	2	0	18	14	0	0	0	0
22	7	0	0	22	24	0	22	10	0	44	40	0	19	3	0
23	0	0	0	11	14	0	3	2	0	31	25	0	0	0	0
24	1	0	0	12	9	0	2	2	0	29	24	0	0	0	0

	SC1			SC3			SC5			SC6			SC8		
Trial	b	d	a	b	d	a	b	d	a	b	d	a	b	d	a
1	0	0	0	0	0	0	16	7	0	6	2	0	10	4	0
2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0
3	38	2	1	0	0	0	0	0	0	0	0	0	0	0	1
4	25	16	0	0	0	0	0	0	0	29	24	0	16	1	0
5	13	15	0	0	0	0	0	0	0	14	27	0	0	0	0
6	0	0	0	0	0	0	0	0	0	8	1	0	1	0	0
7	6	6	1	0	0	0	6	2	0	23	23	0	31	12	0
8	13	12	0	0	0	0	0	0	0	7	13	0	0	0	0
9	3	1	1	0	0	0	0	0	0	0	0	0	1	0	1
10	2	2	1	0	0	0	6	9	0	11	11	0	34	0	1
11	0	4	0	0	0	0	1	0	0	22	30	0	0	0	0
12	2	9	0	0	0	0	0	0	0	0	0	0	3	1	0
13	1	6	0	0	0	0	22	15	0	9	3	0	12	1	0
14	1	6	0	0	0	0	9	16	0	38	34	0	1	7	0
15	6	11	0	1	0	1	3	2	0	0	0	0	2	0	0
16	1	0	0	0	0	0	15	14	0	25	43	0	19	0	1
17	0	0	0	16	0	1	12	20	0	12	27	0	51	43	0
18	9	3	0	11	4	0	2	0	0	0	0	1	14	3	1
19	2	1	1	9	2	0	14	15	0	21	18	0	25	1	1
20	9	5	0	7	2	0	1	1	0	1	0	0	60	31	0
21	8	1	1	15	8	0	0	0	0	0	0	0	0	0	0
22	14	11	1	1	13	0	24	23	0	23	25	0	16	21	0
23	6	7	0	2	3	0	19	12	0	1	1	0	30	26	0
24	6	5	0	0	0	0	6	9	0	1	1	0	0	0	0

Appendix IV: Passive avoidance results

The following tables give the number of operant responses (K) and the number of reinforcements (R) during the presentation of the two tones. On the third (and last) day of discrimination learning, responding during either tone resulted in food reinforcement. During the three days of testing, responding during one tone gave food reinforcement; responding during the other tone resulted in either no reinforcement (control treatment) or the cage being dusted (experimental treatment). All subjects received a total of 48 trials a day; half with the 'food' tone and half with the 'dust' or 'none' tone. The nature of the tone used for 'food' is given at the top of each page (1 = high tone, 2 = low tone).

Bird: TE16
Food Tone: 1

	Discrimination 3		Testing 1		Testing 2		Testing 3	
	Food	Food	Food	Dust	Food	Dust	Food	Dust
Trial	K: R	K: R	K: R	K: R	K: R	K: R	K: R	K: R
1	0: 0		100:10		53: 5		119:10	
2	0: 0		88: 7		0: 0			0: 0
3		0: 0		3: 0	1: 0			0: 0
4		0: 0		0: 0		0: 0	0: 0	
5	79: 8			0: 0		0: 0	0: 0	
6	40: 3		1: 0			2: 0	0: 0	
7		62: 5	4: 0		0: 0			0: 0
8	88: 6		0: 0			0: 0		0: 0
9		23: 1	106:10			0: 0	68: 6	
10		32: 3	68: 6		0: 0		0: 0	
11		47: 8		4: 0	0: 0			0: 0
12	73: 6			1: 0		0: 0		0: 0
13		53: 6	54: 6		0: 0			0: 0
14		36: 3		7: 1		0: 0	63: 8	
15		57: 6	0: 0		0: 0			0: 0
16		48: 3		0: 0		0: 0		0: 0
17	65: 6			0: 0		0: 0	99: 7	
18		23: 4		0: 0	0: 0			0: 0
19	0: 0		0: 0			0: 0		0: 0
20	0: 0			0: 0	0: 0		0: 0	
21	33: 2		0: 0		83: 9		0: 0	
22	56: 7		0: 0		0: 0			0: 0
23		85: 8		0: 0		0: 0	101:10	
24		7: 0	0: 0			0: 0	0: 0	
25	62: 6		72: 7			0: 0		0: 0
26		91: 9	0: 0			0: 0	0: 0	
27		85: 5		0: 0	57: 4		85:10	
28	52: 7			7: 1	53: 3		106: 9	
29	73: 6			0: 0		6: 1		0: 0
30	37: 5		15: 1			0: 0	0: 0	
31	10: 1			0: 0		1: 0		2: 1
32	74: 7		0: 0		0: 0		0: 0	
33		66: 6	0: 0		0: 0		0: 0	
34	85: 6			0: 0	90: 7			0: 0
35	54: 4			2: 0		0: 0		0: 0
36		8: 0	0: 0			0: 0	75: 7	
37		86: 8	0: 0		0: 0			0: 0
38	58: 6			0: 0	0: 0			0: 0
39		5: 1		0: 0		0: 0	0: 0	
40	57: 5		0: 0			0: 0		0: 0
41	74: 9			0: 0	0: 0			0: 0
42	74: 7		91:11			0: 0		0: 0
43		38: 5	117:10			0: 0	30: 5	
44	91: 6			11: 1	0: 0		92: 6	
45		64: 7		0: 0	0: 0			0: 0
46		92: 7	0: 0		0: 0			0: 0
47		60: 5		0: 0	0: 0		118: 9	
48		52: 5		0: 0		1: 0	107:11	

Bird : TE17
Food tone: 1

Trial	Discrimination 3 Food K: R	Discrimination 3 Food K: R	Testing 1 Food K: R	Testing 1 Dust K: R	Testing 2 Food K: R	Testing 2 Dust K: R	Testing 3 Food K: R	Testing 3 Dust K: R
1		8: 0	94: 9		0: 0		48: 5	
2	0: 0		41: 3			0: 0	0: 0	
3	0: 0			0: 0		0: 0	2: 0	
4	23: 3		31: 3		38: 4			0: 0
5		45: 4		18: 1	0: 0			0: 0
6		61: 8		0: 0		0: 0		0: 0
7		0: 0		0: 0	0: 0		0: 0	
8	43: 3		0: 0		16: 1		0: 0	
9		42: 3		0: 0	0: 0			0: 0
10	35: 4			0: 0		0: 0	18: 1	
11		26: 1		0: 0		0: 0	0: 0	
12		0: 0		0: 0		0: 0		0: 0
13	0: 0		0: 0			0: 0	0: 0	
14	0: 0		0: 0		0: 0			0: 0
15	0: 0		55: 4			4: 1		0: 0
16		0: 0		0: 0	17: 1		0: 0	
17	0: 0			0: 0		0: 0		0: 0
18	0: 0			0: 0	0: 0		57: 4	
19		0: 0		0: 0	0: 0		1: 1	
20	0: 0			0: 0		0: 0		0: 0
21	0: 0			5: 0	0: 0			0: 0
22	8: 1		46: 3			0: 0	0: 0	
23	0: 0		55: 7		0: 0			0: 0
24	26: 2			2: 1		0: 0	0: 0	
25		46: 8	0: 0			0: 0	0: 0	
26	52: 4		0: 0			0: 0		0: 0
27	29: 2		0: 0		0: 0			0: 0
28	12: 3		0: 0			0: 0		0: 0
29	67: 6			0: 0		0: 0		0: 0
30		28: 2	0: 0			0: 0		0: 0
31		3: 0	0: 0		0: 0			0: 0
32	25: 3		0: 0		64: 6		0: 0	
33		13: 0		0: 0	0: 0		81: 7	
34		0: 0		0: 0		0: 0	69: 5	
35	69: 5		42: 4			0: 0		1: 0
36	48: 6			0: 0	0: 0		0: 0	
37		32: 5		0: 0		0: 0	0: 0	
38		67: 5	0: 0			0: 0	73: 7	
39		64: 8		0: 0		0: 0		0: 0
40	0: 0		0: 0		0: 0			0: 0
41		65: 5	0: 0		34: 3			0: 0
42		9: 1		0: 0	2: 1		101: 8	
43		34: 2	74: 9			0: 0		0: 0
44		0: 0	43: 5		14: 2		1: 0	
45		55: 6	2: 1		0: 0		88: 8	
46		39: 3		16: 1	42: 4			0: 0
47	55: 5		0: 0			0: 0	0: 0	
48		63: 6		0: 0	0: 0			0: 0

Bird: TE18
Food Tone: 1

Trial	Discrimination 3 Food K: R	Food K: R	Testing 1 Food K: R	Dust K: R	Testing 2 Food K: R	Dust K: R	Testing 3 Food K: R	Dust K: R
1	37: 5		104: 8		5: 1		0: 0	
2	79: 9		60: 8			0: 0	0: 0	
3	97:11		0: 0			0: 0	0: 0	
4	60: 5		0: 0		1: 0		0: 0	
5		8: 0		0: 0	28: 4			0: 0
6	33: 4			1: 1		17: 1		0: 0
7		54: 7		0: 0		0: 0		0: 0
8		125: 9	2: 0			0: 0	0: 0	
9	97: 9		0: 0			2: 0	0: 0	
10		83:11	0: 0			3: 1		0: 0
11	68: 5			0: 0	40: 3		0: 0	
12		70: 4	68: 5			3: 1	0: 0	
13		0: 0		15: 1		0: 0		0: 0
14	0: 0		0: 0		21: 3			0: 0
15		99: 9		0: 0		2: 0		0: 0
16		104:10	0: 0		54: 4		0: 0	
17		78: 8	0: 0		55: 5			0: 0
18	0: 0		0: 0			0: 0	0: 0	
19	26: 4			0: 0	49: 4		0: 0	
20		54: 8		7: 0		0: 0	0: 0	
21	40: 4			0: 0	72: 7			0: 0
22		0: 0		6: 1	67: 6		0: 0	
23	79: 6		0: 0			18: 1	0: 0	
24		80: 9		0: 0	62: 5			0: 0
25		111: 9		0: 0		0: 0	0: 0	
26	132: 7		0: 0			0: 0		0: 0
27	84: 9			0: 0	49: 4		0: 0	
28		108: 8		0: 0	0: 0			0: 0
29		7: 1		0: 0		0: 0	0: 0	
30		37: 3		0: 0		0: 0		0: 0
31		0: 0	0: 0			1: 1		0: 0
32		0: 0	0: 0			0: 0		0: 0
33	46: 9		0: 0		2: 1		0: 0	
34		41: 4	0: 0			9: 0	0: 0	
35		8: 0	0: 0		0: 0		0: 0	
36		0: 0	0: 0		0: 0			0: 0
37	0: 0			0: 0	21: 3			0: 0
38	65: 7		0: 0		35: 4			0: 0
39	0: 0		0: 0			0: 0	0: 0	
40	0: 0			0: 0		0: 0		0: 0
41		0: 0		18: 1	0: 0		0: 0	
42		43: 6	0: 0		17: 0			0: 0
43	105: 8			0: 0	0: 0			0: 0
44	85: 9			0: 0		0: 0		0: 0
45		0: 0		0: 0		0: 0		0: 0
46	103: 9		0: 0		0: 0			0: 0
47	68: 5			1: 1	0: 0		26: 3	
48	3: 0			0: 0	0: 0		37: 4	

Bird: TE19
Food Tone: 2

	Discrimination 3		Testing 1		Testing 2		Testing 3	
	Food	Food	Food	Dust	Food	Dust	Food	Dust
Trial	K: R	K: R	K: R	K: R	K: R	K: R	K: R	K: R
1	16: 4		78: 7		13: 1		57: 5	
2	75: 7		85: 9			0: 0	68: 7	
3	70: 6		81: 8			0: 0	61: 6	
4	76: 7		48: 5		51: 5		61: 4	
5		75: 6		0: 0	43: 7			0: 0
6	23: 3			0: 0		9: 1		0: 0
7		2: 0		0: 0		0: 0		0: 0
8		27: 2	0: 0			1: 0	0: 0	
9	21: 1		0: 0			0: 0	0: 0	
10		21: 2	17: 5			0: 0		0: 0
11	0: 0			0: 0	0: 0		0: 0	
12		1: 0	0: 0			0: 0	0: 0	
13		74: 7		18: 1		0: 0		0: 0
14	52: 6		0: 0		0: 0			0: 0
15		3: 0		5: 1		0: 0		0: 0
16		0: 0	0: 0		0: 0		66: 5	
17		17: 1	0: 0		0: 0			0: 0
18	68: 6		0: 0			0: 0	0: 0	
19	35: 4			19: 1	0: 0		48: 4	
20		48: 3		0: 0		0: 0	67: 8	
21	54: 5			0: 0	0: 0			0: 0
22		32: 4		0: 0	23: 2		0: 0	
23	67: 5		0: 0			0: 0	1: 0	
24		56: 6		0: 0	63: 6			0: 0
25		65: 5		2: 0		0: 0	0: 0	
26	0: 0		67: 5			1: 1		0: 0
27	53: 6			1: 1	44: 3		0: 0	
28		45: 6		0: 0	0: 0			0: 0
29		53: 5		4: 0		0: 0	76: 5	
30		15: 2		14: 1		0: 0		0: 0
31		20: 2	0: 0			0: 0		0: 0
32		48: 4	0: 0			0: 0		0: 0
33	52: 4		0: 0		39: 5		64: 5	
34		49: 6	0: 0			0: 0	81: 8	
35		40: 5	0: 0		54: 8		71: 7	
36		4: 2	0: 0		74:10			0: 0
37	23: 2			0: 0	0: 0			0: 0
38	69: 6		8: 2		50: 7			0: 0
39	78: 7		82: 9			0: 0	75: 7	
40	49: 3			4: 1		0: 0		0: 0
41		57: 4		1: 1	80: 6		19: 1	
42		49: 5	0: 0		72: 9			0: 0
43	42: 4			0: 0	63: 7			2: 0
44	3: 0			0: 0		0: 0		0: 0
45		62: 6		0: 0		0: 0		0: 0
46	1: 0		1: 1		0: 0			1: 0
47	54: 4			1: 0	0: 0		78: 6	
48	37: 3			1: 0	0: 0		8: 2	

Bird: TE20
Food Tone: 2

Trial	Discrimination 3 Food K: R	Discrimination 3 Food K: R	Testing 1 Food K: R	Testing 1 Dust K: R	Testing 2 Food K: R	Testing 2 Dust K: R	Testing 3 Food K: R	Testing 3 Dust K: R
1	93: 7		102: 9		3: 1		83: 8	
2		85: 8	81: 7		0: 0			13: 1
3		88: 6		3: 1	0: 0		80: 6	
4	68: 6		0: 0		0: 0		0: 0	
5		0: 0		0: 0		0: 0	0: 0	
6	53: 4		0: 0			0: 0	0: 0	
7		0: 0	4: 0			1: 0	0: 0	
8		0: 0	0: 0			0: 0	0: 0	
9		0: 0		0: 0	69: 6			0: 0
10		54: 4		0: 0		2: 0	0: 0	
11	1: 0		32: 4		0: 0		0: 0	
12		53: 5		20: 1	1: 0			0: 0
13	32: 3		0: 0			0: 0		0: 0
14	61: 3			0: 0	0: 0		0: 0	
15		57: 6	1: 0			0: 0		1: 0
16		17: 1		1: 0		0: 0		0: 0
17	37: 4			3: 1	76: 7			0: 0
18	0: 0			0: 0	62:10			0: 0
19	42: 4			0: 0	0: 0		0: 0	
20		51: 5	2: 0		0: 0			0: 0
21	0: 0		0: 0		0: 0		90: 8	
22	26: 1		0: 0			0: 0	0: 0	
23	45: 7			2: 0	0: 0			0: 0
24		0: 0	64: 5			0: 0		0: 0
25		20: 1		3: 1	11: 2			0: 0
26	73: 6			1: 1		2: 0	0: 0	
27		61: 5	0: 0		0: 0		0: 0	
28	55: 4			0: 0		9: 0		0: 0
29		42: 3	0: 0			0: 0	10: 0	
30		0: 0	0: 0		0: 0		50: 5	
31		46: 5		0: 0	0: 0		0: 0	
32		0: 0		0: 0		0: 0		0: 0
33		2: 1	0: 0		4: 1			0: 0
34	65: 6			3: 0		13: 1	0: 0	
35	57: 8			2: 0	34: 4		0: 0	
36		34: 2		4: 1		2: 0		2: 0
37	0: 0		0: 0			0: 0		0: 0
38		35: 3		1: 0	0: 0		47: 4	
39		68: 5	66: 6			0: 0	0: 0	
40	36: 3			0: 0		0: 0		0: 0
41	51: 6		0: 0			0: 0		0: 0
42	42: 5		0: 0		85: 8		0: 0	
43	44: 3			0: 0		0: 0		0: 0
44		35: 2		1: 0		0: 0	0: 0	
45		51: 7		1: 0	62: 5			0: 0
46	49: 4		58: 8		77: 7			0: 0
47	35: 3		0: 0			0: 0		1: 0
48	0: 0		58: 7			0: 0		0: 0

Bird: SE16
Food Tone: 2

Trial	Discrimination 3 Food K: R	Discrimination 3 Food K: R	Testing 1 Food K: R	Testing 1 Dust K: R	Testing 2 Food K: R	Testing 2 Dust K: R	Testing 3 Food K: R	Testing 3 Dust K: R
1	47: 4		68: 6		91: 8		85:10	
2	110: 9		77: 7			8: 1		0: 0
3		103: 8		6: 1		1: 0	82: 6	
4	120: 8		91: 9		0: 0		67: 7	
5		59: 9		7: 1		0: 0	85: 7	
6		80: 8		0: 0		0: 0		0: 0
7	0: 0		65: 6		79: 6		26: 2	
8	0: 0			0: 0	55: 6			0: 0
9		61: 4	36: 3		48: 4			0: 0
10	0: 0		2: 1		36: 5			0: 0
11	0: 0			0: 0		20: 1		0: 0
12	0: 0			0: 0		0: 0	78: 6	
13	13: 2			0: 0		0: 0	89: 7	
14		88: 7	118: 7		3: 0			1: 0
15		0: 0	89: 9			2: 0		0: 0
16		80: 9		1: 1	0: 0			0: 0
17	84: 9			0: 0	68: 6			0: 0
18	94: 9		85: 8			1: 0	16: 2	
19	0: 0		57: 6			0: 0		1: 0
20	65: 6		77: 6		79: 8			0: 0
21		113:10		2: 0		0: 0	73: 7	
22	105: 9		0: 0			4: 0		0: 0
23	0: 0			0: 0	18: 2		101: 8	
24		0: 0		0: 0	75: 8		96:10	
25		0: 0		1: 1	109: 9			0: 0
26	0: 0		0: 0			0: 0	61: 6	
27		0: 0		0: 0	0: 0		85:10	
28		0: 0		0: 0		0: 0		0: 0
29	75: 9		57: 6			0: 0	50: 6	
30	62: 5		59: 6		63: 6			0: 0
31	78: 8			0: 0	79: 9		77: 8	
32		0: 0		0: 0	36: 2			0: 0
33		53: 5		0: 0		0: 0		0: 0
34		77: 8	0: 0			0: 0		0: 0
35		94: 8	0: 0			0: 0		0: 0
36	0: 0			0: 0	53: 6		40: 4	
37		0: 0	5: 0		7: 0		83: 6	
38	81: 8		64: 8			1: 0	112:10	
39		0: 0		8: 1	21: 3			0: 0
40	51: 5		7: 0			2: 0		0: 0
41	97: 9			0: 0		0: 0		0: 0
42		112: 9		0: 0	49: 4		12: 1	
43		0: 0	45: 5			5: 1	80: 6	
44		0: 0		7: 0		0: 0	105:10	
45		50: 5	73: 5		0: 0			0: 0
46		22: 3	100: 8		87: 8		80: 6	
47	0: 0			3: 0	80: 6		88:10	
48		0: 0	87: 7			0: 0	81: 8	

Bird: SE17
Food Tone: 2

	Discrimination 3		Testing 1		Testing 2		Testing 3	
	Food	Food	Food	Dust	Food	Dust	Food	Dust
Trial	K: R	K: R	K: R	K: R	K: R	K: R	K: R	K: R
1	0: 0		79: 8		0: 0		0: 0	
2	59: 6		113: 8		0: 0		0: 0	
3		69: 6		3: 1	0: 0		0: 0	
4		21: 1		0: 0		0: 0		0: 0
5	93: 6			0: 0	0: 0		0: 0	
6		95: 6	0: 0		0: 0		0: 0	
7	61: 9			0: 0		0: 0		0: 0
8		43: 2	0: 0			0: 0		0: 0
9		32: 5		0: 0		0: 0		0: 0
10	38: 4			0: 0	51: 5		0: 0	
11	0: 0		0: 0		1: 0		66: 5	
12		2: 0	0: 0			4: 0		0: 0
13		0: 0	0: 0		0: 0		0: 0	
14		101: 9	0: 0			0: 0		0: 0
15		6: 0	6: 0			0: 0		0: 0
16		65: 4		12: 1		8: 0		0: 0
17	0: 0			0: 0		2: 1		0: 0
18	1: 0			0: 0	0: 0		0: 0	
19	0: 0			0: 0	0: 0		3: 0	
20		0: 0	0: 0			0: 0	0: 0	
21	51: 4		0: 0		0: 0		86: 7	
22	55: 6		0: 0		0: 0		8: 3	
23		0: 0	0: 0		0: 0			0: 0
24		0: 0		0: 0		0: 0		1: 0
25	0: 0			0: 0		0: 0		0: 0
26	36: 5			0: 0		0: 0	0: 0	
27		27: 3		0: 0	0: 0			0: 0
28		35: 3		0: 0	0: 0		67: 6	
29		34: 6		0: 0	0: 0		103: 9	
30	0: 0		0: 0		0: 0			0: 0
31	0: 0		0: 0			0: 0		0: 0
32	0: 0		0: 0			0: 0	0: 0	
33		0: 0		0: 0		0: 0	0: 0	
34		0: 0	0: 0			0: 0	0: 0	
35	0: 0			0: 0		0: 0		0: 0
36	0: 0			0: 0		0: 0		0: 0
37		65: 6	0: 0		0: 0			0: 0
38		42: 6	0: 0		0: 0			0: 0
39	84: 9		0: 0			0: 0	0: 0	
40		0: 0		0: 0		0: 0		0: 0
41		0: 0		0: 0	0: 0		0: 0	
42	0: 0			0: 0		0: 0		0: 0
43		0: 0		0: 0	0: 0			0: 0
44	10: 1		0: 0		12: 0			0: 0
45	87: 6			0: 0	0: 0			1: 0
46	83: 6		0: 0		0: 0		104: 8	
47		0: 0	2: 0			1: 0	0: 0	
48	0: 0		0: 0			0: 0	0: 0	

Bird: SE18
Food Tone: 1

Trial	Discrimination 3 Food K: R	Discrimination 3 Food K: R	Testing 1 Food K: R	Testing 1 Dust K: R	Testing 2 Food K: R	Testing 2 Dust K: R	Testing 3 Food K: R	Testing 3 Dust K: R
1	68: 7		77: 8		45: 6		45: 7	
2	79: 8			5: 1	63: 5			0: 0
3		76: 5		10: 1	51: 5			0: 0
4		61: 6		0: 0	1: 0			1: 0
5		57: 7		0: 0		0: 0	13: 3	
6	94: 7			19: 1		0: 0		0: 0
7		71: 7	0: 0		0: 0			0: 0
8		5: 1		0: 0	0: 0			0: 0
9		13: 2	0: 0		0: 0			0: 0
10	1: 1			0: 0		0: 0	0: 0	
11	2: 0			2: 0	0: 0		0: 0	
12		2: 1	0: 0			0: 0	0: 0	
13	55: 5		0: 0		0: 0			0: 0
14		3: 0		8: 0	0: 0		15: 2	
15		2: 0	9: 1			0: 0		0: 0
16	1: 0		0: 0		0: 0			0: 0
17		0: 0	0: 0			3: 0		0: 0
18		0: 0		7: 0	0: 0			0: 0
19	2: 0		0: 0		0: 0		2: 0	
20		86: 6	40: 2		0: 0			0: 0
21	46: 7		0: 0		0: 0		0: 0	
22	1: 0		0: 0			0: 0	24: 1	
23		15: 1		1: 1		0: 0	55: 6	
24		2: 0	13: 2			0: 0	42: 5	
25		0: 0		0: 0		1: 1	15: 1	
26	0: 0			0: 0		0: 0		1: 1
27	0: 0			0: 0		0: 0		4: 0
28	0: 0		0: 0		0: 0			0: 0
29		0: 0	0: 0		0: 0			0: 0
30		0: 0		0: 0		0: 0	0: 0	
31		1: 0	0: 0		0: 0			0: 0
32	0: 0		0: 0			0: 0	0: 0	
33	0: 0			0: 0		0: 0	0: 0	
34	0: 0			0: 0	3: 0			0: 0
35	1: 1		0: 0			2: 1	0: 0	
36	0: 0			1: 1		0: 0	0: 0	
37	0: 0			0: 0		0: 0	0: 0	
38	0: 0		0: 0		0: 0		0: 0	
39	0: 0			0: 0		0: 0	0: 0	
40		0: 0	0: 0		0: 0			0: 0
41		0: 0		0: 0	0: 0		14: 0	
42		0: 0	0: 0		0: 0		0: 0	
43	0: 0			0: 0		0: 0	0: 0	
44	0: 0			0: 0		0: 0		0: 0
45		0: 0		0: 0	0: 0			0: 0
46		0: 0	6: 0			0: 0	0: 0	
47		0: 0	0: 0			0: 0		0: 0
48	0: 0		0: 0			0: 0		0: 0

Bird: SE19
Food Tone: 2

Trial	Discrimination 3 Food K: R	Discrimination 3 Food K: R	Testing 1 Food K: R	Testing 1 Dust K: R	Testing 2 Food K: R	Testing 2 Dust K: R	Testing 3 Food K: R	Testing 3 Dust K: R
1	87: 7		91:12		0: 0		0: 0	
2	73: 6		51: 6			0: 0	0: 0	
3	80:10		0: 0			0: 0	0: 0	
4	64: 5		0: 0		0: 0		0: 0	
5		65: 7		10: 1	0: 0			0: 0
6	62: 5			1: 1		0: 0		0: 0
7		95:11		0: 0		0: 0		0: 0
8		0: 0	0: 0			0: 0	0: 0	
9	0: 0		0: 0			0: 0	0: 0	
10		54: 5	3: 0			0: 0		0: 0
11	0: 0			5: 0	0: 0		0: 0	
12		53: 4	0: 0			0: 0	0: 0	
13		93:11		3: 1		0: 0		0: 0
14	0: 0		0: 0		0: 0			0: 0
15		122:10		0: 0		0: 0		0: 0
16		116:12	0: 0		0: 0		0: 0	
17		0: 0	0: 0		0: 0			0: 0
18	100: 7		0: 0			0: 0	0: 0	
19	0: 0			0: 0	0: 0		0: 0	
20		0: 0		0: 0		0: 0	0: 0	
21	102: 9			2: 0	0: 0			0: 0
22		117:10		0: 0	0: 0		0: 0	
23	0: 0		18: 1			0: 0	0: 0	
24		0: 0		1: 1	0: 0			0: 0
25		35: 2		0: 0		0: 0	0: 0	
26	70: 7		0: 0			0: 0		0: 0
27	0: 0			0: 0	0: 0		0: 0	
28		100: 9		0: 0	0: 0			0: 0
29		41: 4		0: 0		0: 0	0: 0	
30		48: 7		0: 0		0: 0		0: 0
31		0: 0	0: 0			0: 0		0: 0
32		0: 0	0: 0			0: 0		0: 0
33	0: 0		0: 0		0: 0		0: 0	
34		17: 1	0: 0			0: 0	0: 0	
35		0: 0	0: 0		0: 0		0: 0	
36		0: 0	0: 0		0: 0			0: 0
37	0: 0			0: 0	0: 0			0: 0
38	72: 7		0: 0		0: 0			0: 0
39	80:12		2: 0			0: 0	0: 0	
40	36: 4			1: 0		0: 0		0: 0
41		82: 6		11: 1	0: 0		0: 0	
42		105: 9	0: 0		0: 0			0: 0
43	0: 0			0: 0	0: 0			0: 0
44	29: 4			0: 0		0: 0		0: 0
45		0: 0		0: 0		0: 0		0: 0
46	0: 0		0: 0		0: 0			0: 0
47	102:10			0: 0	0: 0		0: 0	
48	88: 8			0: 0	0: 0		0: 0	

Bird: SE20
Food Tone: 1

Trial	Discrimination 3 Food K: R	Food K: R	Testing 1 Food K: R	Dust K: R	Testing 2 Food K: R	Dust K: R	Testing 3 Food K: R	Dust K: R
1	77: 8		82: 9		0: 0		0: 0	
2	82: 6		77: 8			0: 0	0: 0	
3	48: 5		27: 1			0: 0	0: 0	
4	3: 0		29: 2		17: 2		0: 0	
5		43: 3		0: 0	0: 0			0: 0
6	2: 1			0: 0		11: 0		1: 1
7		0: 0		1: 1		0: 0		0: 0
8		0: 0	0: 0			0: 0	0: 0	
9	27: 3		0: 0			0: 0	0: 0	
10		8: 1	0: 0			0: 0		0: 0
11	20: 3			0: 0	0: 0		0: 0	
12		0: 0	0: 0			0: 0	0: 0	
13		61: 6		0: 0		0: 0		0: 0
14	34: 4		0: 0		0: 0			0: 0
15		51: 4		0: 0		0: 0		0: 0
16		12: 3	0: 0		14: 2		0: 0	
17		22: 3	0: 0		32: 2			0: 0
18	45: 5		0: 0			4: 1	0: 0	
19	36: 3			0: 0	0: 0		0: 0	
20		25: 3		0: 0		0: 0	0: 0	
21	41: 3			0: 0	0: 0			0: 0
22		20: 2		0: 0	0: 0		0: 0	
23	42: 5		0: 0			0: 0	0: 0	
24		38: 3		0: 0	0: 0			0: 0
25		0: 0		0: 0		0: 0	0: 0	
26	0: 0		0: 0			0: 0		0: 0
27	55: 5			0: 0	0: 0		0: 0	
28		0: 0		0: 0	0: 0			0: 0
29		0: 0		0: 0		0: 0	0: 0	
30		27: 5		0: 0		0: 0		0: 0
31		0: 0	0: 0			0: 0		0: 0
32		0: 0	0: 0			0: 0		0: 0
33	0: 0		0: 0		0: 0		0: 0	
34		34: 2	0: 0			0: 0	0: 0	
35		0: 0	0: 0		0: 0		0: 0	
36		31: 4	0: 0		0: 0			0: 0
37	10: 1			0: 0	0: 0			0: 0
38	0: 0		0: 0		0: 0			0: 0
39	0: 0		0: 0			0: 0	0: 0	
40	79: 7			0: 0		11: 0		0: 0
41		64: 8		0: 0	21: 2		0: 0	
42		0: 0	0: 0		5: 1			0: 0
43	74: 6			0: 0	45: 3			0: 0
44	35: 2			0: 0		0: 0		0: 0
45		50: 4		0: 0		0: 0		8: 0
46	33: 2		0: 0		0: 0			0: 0
47	15: 1			0: 0	0: 0		0: 0	
48	0: 0			0: 0	0: 0		0: 0	

Bird: TC16
Food Tone: 1

Trial	Discrimination 3 Food K: R	Food K: R	Testing 1 Food K: R	None K: R	Testing 2 Food K: R	None K: R	Testing 3 Food K: R	None K: R
1	74: 7		81: 8		108: 9		111:10	
2	22: 2		86: 8			3: 1		11: 1
3		0: 0		0: 0	114: 7			6: 1
4		88: 7		3: 0	101: 6			7: 1
5	91: 7			3: 0		3: 1		14: 1
6		69: 7		12: 1		5: 1		5: 1
7		74: 8	0: 0		58: 8		92:10	
8	71: 7		0: 0			17: 1	99: 9	
9	59: 5		0: 0			3: 1	93: 9	
10	53: 5			0: 0	108: 9			2: 1
11	10: 0		76: 9			12: 1		5: 1
12	44: 3		72: 9		87: 7			12: 1
13	0: 0			20: 1		11: 1	101: 9	
14	65: 9			0: 0		9: 1	91: 8	
15	70: 7			8: 1	93: 9			3: 1
16		0: 0		9: 1	77: 8			3: 1
17	29: 3			1: 1		7: 1	91: 8	
18		4: 0		4: 1		0: 0		5: 0
19		45: 5	109: 8			18: 1	50: 5	
20	67: 5			8: 1	65: 5			3: 1
21	55: 7		93: 9		99: 7		38: 4	
22		0: 0	77: 8			3: 1		8: 1
23	89: 9			7: 1	89: 8			9: 1
24		68: 8	0: 0			15: 1	53: 5	
25		58: 6		0: 0	82: 8			5: 1
26	85: 8		85: 8		67:10			11: 1
27	79: 7			12: 1		11: 1	59: 5	
28	85: 6			8: 1	79: 8			0: 0
29	95: 6			12: 1		6: 1	47: 3	
30		0: 0	90: 8		100: 8		8: 0	
31		0: 0		15: 1	97: 8			0: 0
32		0: 0	69: 7		98: 8		2: 0	
33		0: 0	80:11			0: 0	4: 1	
34		0: 0	102: 9		73: 8			0: 0
35		0: 0	105: 9			14: 1	0: 0	
36		64: 8	106:10		53: 6		43: 3	
37	68: 7		90: 9		95:10		72: 9	
38		66: 7		20: 1	88: 7		79: 7	
39	87: 7			11: 1		16: 1		1: 1
40	43: 5		87: 8			16: 1	71: 5	
41		23: 2	80:11			2: 1	15: 0	
42		72: 6		20: 1	89: 7			0: 0
43		0: 0	0: 0		109:10			1: 1
44	72: 7			0: 0	107: 9		0: 0	
45	89: 7			19: 1		19: 1		0: 0
46		80: 6		7: 1		1: 1	18: 1	
47		90: 9	115: 8			0: 0	98: 8	
48		45: 4	102:10			16: 1		3: 1

Bird: TC17
Food Tone: 2

Trial	Discrimination 3 Food K: R	Discrimination 3 Food K: R	Testing 1 Food K: R	Testing 1 None K: R	Testing 2 Food K: R	Testing 2 None K: R	Testing 3 Food K: R	Testing 3 None K: R
1	79:10		59: 7		92: 9		75:12	
2	93: 8		66: 9		107: 9			3: 1
3	71: 9			11: 1		11: 1		12: 1
4		83: 7		16: 1	65: 7		87:10	
5	70: 6			4: 0	86: 7			18: 1
6	91: 8			0: 0		6: 1		12: 1
7		79: 7	46: 3		86: 8			15: 1
8	107: 9		0: 0		77: 6		77: 7	
9		84: 6	51: 5		51:10		87: 9	
10	9: 2		64: 7			4: 1	73: 9	
11	0: 0		78: 8			13: 1	32: 2	
12		29: 4	65: 7		79: 6			0: 0
13		82: 9		4: 1		1: 1	0: 0	
14	63: 8		71: 7			11: 1		1: 1
15		84: 8		9: 1		8: 1		1: 1
16		2: 0	81: 7			6: 1		9: 1
17		0: 0		12: 1		3: 1		2: 1
18	0: 0			12: 1		20: 1		10: 1
19	58: 8		68:10		82: 8		81: 6	
20	0: 0		71: 9		72: 7		99: 8	
21	0: 0			15: 1	89: 8			9: 1
22	68: 8		83: 7		75: 7		88: 8	
23	88: 9		81: 6			8: 1	74:10	
24		73: 9	79: 8		77: 8		109: 8	
25	91: 9			10: 1		13: 1		16: 1
26		89:11		14: 1		16: 1	94:10	
27		43: 5		7: 1		16: 1		18: 1
28		103: 8		3: 1		12: 1		18: 1
29	91: 9		71: 8		80: 7		81: 6	
30	112:10			14: 1		11: 1		2: 1
31		98: 8		4: 1	92: 6		96: 8	
32		96: 7	102:11			2: 1		8: 1
33		0: 0		0: 0	91: 7		77:10	
34	87: 8			8: 1	84: 8			16: 1
35	100: 8			18: 1	86: 8		87: 8	
36		99: 9	93: 7		95: 7		86: 9	
37		76: 9	75: 7			9: 1		8: 1
38	102: 8			7: 1	81: 7			0: 0
39		52: 8	82: 8		71: 5		0: 0	
40		90: 7		10: 1		3: 1		0: 0
41	77: 7			10: 1	103: 7		58: 5	
42		0: 0	83: 6		89: 8		73: 8	
43	98: 7		69: 7		96: 7		69: 6	
44		71: 9	81: 8			12: 1		7: 1
45	74: 9			20: 1		7: 1		2: 1
46		100: 8		9: 1		7: 1		5: 1
47		97: 8	78:10			17: 1	54: 4	
48		102: 7		16: 1		1: 1	87: 8	

Bird: TC18
Food Tone: 2

Trial	Discrimination 3 Food K: R	Discrimination 3 Food K: R	Testing 1 Food K: R	Testing 1 None K: R	Testing 2 Food K: R	Testing 2 None K: R	Testing 3 Food K: R	Testing 3 None K: R
1	83: 11		0: 0		0: 0		0: 0	
2	95: 8		34: 5		1: 1			1: 1
3	82: 9			16: 1		1: 0		2: 0
4		76: 7		0: 0	1: 1		27: 5	
5	44: 7			0: 0	0: 0			17: 1
6	72: 9			15: 1		0: 0		10: 1
7		78: 6	0: 0		0: 0			20: 1
8	79: 7		0: 0		1: 1		73: 6	
9		76: 7	0: 0		1: 1		62: 7	
10	16: 3		0: 0			17: 1	87: 8	
11	44: 3		0: 0			7: 0	103: 7	
12		60: 8	0: 0		74: 5			5: 1
13		60: 5		0: 0		2: 1	78: 7	
14	1: 0		0: 0			16: 1		11: 1
15		0: 0		0: 0		1: 1		1: 1
16		0: 0	0: 0			2: 1		20: 1
17		8: 0		0: 0		4: 1		8: 1
18	0: 0			0: 0		7: 1		2: 1
19	40: 4		0: 0		48: 8		51: 4	
20	36: 3		0: 0		57: 5		59: 5	
21	61: 6			1: 1	63: 7			1: 0
22	74: 7		0: 0		73: 8		61: 4	
23	84: 8		17: 1			4: 1	50: 3	
24		78: 6	61: 4		66: 5		57: 6	
25	32: 2			10: 1		5: 1		11: 1
26		0: 0		0: 0		7: 1	88: 8	
27		0: 0		0: 0		5: 1		0: 0
28		0: 0		11: 1		6: 1		0: 0
29	85: 7		0: 0		58: 4		61: 5	
30	65: 8			0: 0		2: 1		5: 0
31		59: 6		0: 0	73: 7		76: 8	
32		8: 0	47: 5			1: 1		8: 1
33		56: 6		10: 1	68: 7		19: 1	
34	62: 5			19: 1	44: 5			0: 0
35	7: 0			2: 1	79: 7		75: 8	
36		50: 6	36: 3		78: 6			0: 0
37		89: 6	64: 5			7: 1		0: 0
38	2: 0			17: 1	69: 8			6: 1
39		68: 6	56: 7		83: 6		76: 7	
40		52: 7		19: 1		3: 1	40: 4	
41	0: 0			0: 0	60: 7		87: 9	
42		0: 0	45: 4		66: 6		76: 9	
43	0: 0		69: 4		66: 7		83: 8	
44		10: 0	63: 6			2: 1		16: 1
45	51: 5			16: 1		1: 1		4: 1
46		54: 6		3: 1		3: 1		8: 1
47		37: 3	40: 4			17: 1	89: 7	
48		0: 0		0: 0		1: 1	73: 10	

Bird: TC19
Food Tone: 1

Trial	Discrimination 3 Food K: R	Discrimination 3 Food K: R	Testing 1 Food K: R	Testing 1 None K: R	Testing 2 Food K: R	Testing 2 None K: R	Testing 3 Food K: R	Testing 3 None K: R
1	88: 9		43: 9		40: 6		61: 7	
2	102: 8		57: 6		53: 7			2: 1
3	79: 8		79: 7		33: 4		0: 0	
4	95: 9			6: 1	7: 0			5: 1
5	0: 0			16: 1	55: 4		40: 3	
6	0: 0			5: 1		2: 1		13: 1
7		0: 0	46: 5			17: 1		10: 1
8	30: 7		15: 0		55: 4		45: 5	
9	62: 8			3: 1		3: 1	40: 7	
10		42: 7	65: 6			19: 1	30: 4	
11	92: 9			2: 1		1: 1		8: 1
12	0: 0		48: 9			12: 1		6: 1
13		0: 0		4: 1		14: 1	47: 7	
14		74: 7	84: 7			3: 1		4: 1
15	0: 0			9: 1	74: 6			0: 0
16		81: 9		2: 1	73: 6		0: 0	
17	1: 0			0: 0		19: 1		18: 1
18		0: 0	0: 0		40: 6			4: 1
19	0: 0			20: 1		16: 1		9: 1
20	0: 0			10: 1	52: 6		76: 5	
21	80: 8		87: 7			15: 1		1: 1
22		0: 0	74: 8			18: 1		13: 1
23		14: 0		1: 1	28: 2		50: 4	
24		0: 0		12: 1	53: 5		60: 5	
25		5: 1	22: 3			14: 1	25: 3	
26	61: 7		70: 7			3: 1		3: 1
27	90: 7		66: 8		70: 6			13: 1
28		65: 7	76: 7			6: 1	51: 4	
29	85: 6		58: 8		59: 5		45: 5	
30		62: 7	26: 3		57: 7			9: 1
31		98: 7		5: 1	65: 6		0: 0	
32		0: 0		0: 0	51: 8			0: 0
33		56: 5		12: 1		0: 0	19: 2	
34		67: 8		6: 1	56: 5		34: 3	
35		79: 9	68: 7			4: 1		19: 1
36		0: 0	75: 6		55: 5		55: 5	
37		81: 9	68: 8		32: 3		57: 5	
38	0: 0		51: 5			11: 1		18: 1
39	73: 6			6: 1		0: 0	57: 4	
40	26: 3		73: 8		0: 0			7: 1
41		12: 0		9: 1	0: 0			1: 1
42	0: 0			4: 1	34: 2		58: 5	
43	0: 0			7: 1		1: 1		14: 1
44		76: 8	58: 6			1: 1	48: 3	
45	24: 1			0: 0		1: 1	33: 4	
46		0: 0	22: 3			0: 0	8: 2	
47		32: 3		4: 1		3: 1		15: 1
48		0: 0		7: 1	44: 3			6: 1

Bird: TC20
Food Tone: 2

Trial	Discrimination 3 Food K: R	Discrimination 3 Food K: R	Testing 1 Food K: R	Testing 1 None K: R	Testing 2 Food K: R	Testing 2 None K: R	Testing 3 Food K: R	Testing 3 None K: R
1	65: 8		92: 8		80:10		127:11	
2		96: 9	91:10		111: 6			16: 1
3		91: 6		6: 1	74:11		82:10	
4	46: 6		103: 8		26: 2		95: 9	
5		110: 9		0: 0		15: 1	107: 8	
6	79: 8		0: 0			5: 1	71: 6	
7		0: 0	0: 0			3: 1	0: 0	
8		0: 0	78: 5			3: 1	0: 0	
9		0: 0		8: 1	131: 9			0: 0
10		32: 3		14: 1		2: 1	0: 0	
11	79: 8		112: 9		96: 8		26: 2	
12		92: 8		4: 1	113: 8			0: 0
13	119:11		83: 8			9: 1		0: 0
14	74: 8			14: 1	91: 9		0: 0	
15		43: 4	83:10			4: 1		10: 1
16		96:10		13: 1		18: 1		4: 1
17	0: 0			10: 1	118:10			2: 1
18	0: 0			7: 1	90:10			15: 1
19	45: 7			17: 1	111: 9		124: 8	
20		54: 5	117: 9		95:11			3: 1
21	95: 9		87: 8		104:10		47: 5	
22	122:10		4: 1			13: 1	89: 7	
23	120:11			3: 1	107:11			11: 1
24		82: 8	101: 8			16: 1		0: 0
25		99:11		0: 0	104:11			7: 1
26	120:10			6: 1		7: 1	118:12	
27		80: 9	114: 9		106:10		120:10	
28	79: 6			1: 1		1: 1		5: 1
29		0: 0	97: 7			14: 1	98: 9	
30		83: 8	97: 9		109:10		87: 8	
31		118: 9		2: 1	122:11		66: 6	
32		77: 7		16: 1		17: 1		17: 1
33		57: 5	126: 9		90: 9			8: 1
34	37: 5			6: 1		9: 1	86: 9	
35	118:13			17: 1	36: 8		103:10	
36		101:10		16: 1		2: 1		5: 1
37	67: 6		102:11			6: 1		7: 1
38		5: 0		11: 1	59: 5		0: 0	
39		115: 9	106: 9			10: 1	53: 6	
40	99:10			8: 1		10: 1		10: 1
41	0: 0		86:11			15: 1		11: 1
42	92: 8		92: 7		92: 9		60: 5	
43	9: 1			1: 1		17: 1		8: 1
44		63: 5		12: 1		6: 1	73: 7	
45		57: 6		14: 1	90: 7			5: 1
46	1: 0		128:11		66: 6			12: 1
47	3: 0		119:10			6: 1		4: 1
48	3: 0		86: 8			15: 1		16: 1

Bird: SC16
Food Tone: 1

Trial	Discrimination 3 Food K: R	Discrimination 3 Food K: R	Testing 1 Food K: R	Testing 1 None K: R	Testing 2 Food K: R	Testing 2 None K: R	Testing 3 Food K: R	Testing 3 None K: R
1	106:11		135:11		110:11		106:11	
2	122:10			19: 1	136:11		122:10	
3		148:10	87: 8			14: 1		18: 1
4		111:13		7: 1		5: 1		18: 1
5	104:12		0: 0			5: 1		18: 1
6		134:12	87: 6			20: 1	69: 7	
7		129:12		7: 1		12: 1		9: 1
8		117:11	0: 0			3: 1	29: 3	
9	30: 5			0: 0	0: 0		71: 8	
10	0: 0			18: 1	105:10			13: 1
11		83: 8	0: 0		132:12			8: 1
12		103: 9		0: 0	107: 9			0: 0
13		136:12	0: 0			0: 0	106:10	
14	101:12			4: 0		0: 0	121:10	
15	8: 2			16: 1	0: 0			0: 0
16		0: 0		0: 0		0: 0	0: 0	
17	0: 0		0: 0		0: 0			4: 1
18	0: 0			0: 0	42: 3		27: 2	
19	0: 0		1: 0		117:12			9: 1
20		1: 0		0: 0		0: 0	37: 4	
21	7: 1		7: 0			0: 0	55: 6	
22		124:11		0: 0		0: 0		0: 0
23	115:12		21: 4			0: 0		18: 1
24	0: 0			3: 1	0: 0		105: 9	
25		0: 0		0: 0	0: 0			0: 0
26	0: 0			0: 0		8: 1	117:10	
27		6: 0	0: 0		0: 0		91: 9	
28	0: 0		0: 0		0: 0		98:13	
29	59: 5		0: 0		0: 0			0: 0
30		10: 1		0: 0		0: 0	0: 0	
31	0: 0		0: 0		100:10			14: 1
32		0: 0		0: 0		0: 0		1: 1
33	0: 0		0: 0			0: 0		0: 0
34	0: 0			12: 1		0: 0	0: 0	
35	0: 0			0: 0	49: 6			0: 0
36		0: 0	0: 0		0: 0			14: 1
37		0: 0	45: 4		60: 7		56: 4	
38		0: 0		3: 1	93: 9		116: 9	
39	0: 0		0: 0		0: 0		59: 6	
40		0: 0	0: 0			0: 0		0: 0
41	21: 2			13: 1		0: 0		0: 0
42		0: 0	92: 9		0: 0			0: 0
43		0: 0		5: 1		0: 0	96: 9	
44		0: 0	87: 9			0: 0	105:11	
45		0: 0	107: 8		13: 0		65: 6	
46		0: 0		2: 1		0: 0		7: 1
47	0: 0			8: 1		0: 0		0: 0
48	5: 1		0: 0		0: 0		0: 0	

Bird: SC17
Food Tone: 1

Trial	Discrimination 3 Food K: R	Discrimination 3 Food K: R	Testing 1 Food K: R	Testing 1 None K: R	Testing 2 Food K: R	Testing 2 None K: R	Testing 3 Food K: R	Testing 3 None K: R
1	12: 2		22: 2		15: 3		28: 4	
2	0: 0		17: 3		35: 4			7: 1
3	7: 3			20: 1		11: 1		5: 1
4		29: 2		0: 0	14: 4		43: 2	
5	31: 2			0: 0	30: 3			8: 1
6	29: 1			0: 0		14: 1		9: 1
7		30: 5	0: 0		0: 0			10: 1
8	37: 3		0: 0		0: 0		24: 2	
9		35: 3	0: 0		0: 0		35: 4	
10	43: 5		0: 0			1: 1	44: 3	
11	17: 1		0: 0			0: 0	30: 4	
12		59: 4	0: 0		0: 0			15: 1
13		41: 4		0: 0		0: 0	58: 4	
14	46: 4		0: 0			0: 0		3: 1
15		14: 1		0: 0		0: 0		1: 1
16		26: 1	0: 0			8: 1		18: 0
17		29: 2		0: 0		0: 0		1: 1
18	32: 3			0: 0		0: 0		5: 1
19	40: 2		0: 0		2: 0			0: 0
20	25: 2		0: 0		17: 0		0: 0	
21	17: 1			0: 0	14: 1			0: 0
22	24: 4		0: 0		24: 2		28: 2	
23	15: 1		0: 0			9: 1	32: 5	
24		25: 3	0: 0		0: 0		44: 4	
25	29: 3			0: 0		0: 0		4: 1
26		36: 4		0: 0		0: 0	41: 5	
27		41: 2		5: 0		0: 0		11: 1
28		29: 2		0: 0		0: 0		6: 1
29	44: 4		0: 0		5: 0		50: 5	
30	34: 3			0: 0		7: 1		8: 1
31		37: 1		0: 0	0: 0		56: 3	
32		26: 3	0: 0			9: 1		9: 1
33		41: 4		0: 0	0: 0		24: 4	
34	18: 2			0: 0	0: 0			10: 1
35	28: 4			0: 0	8: 0		39: 5	
36		21: 2	0: 0		20: 3		35: 3	
37		26: 2	0: 0			12: 1		4: 1
38	28: 3			2: 0	17: 1			14: 1
39		0: 0	0: 0		21: 2		35: 2	
40		7: 1		0: 0		4: 1	35: 4	
41	31: 2			0: 0	0: 0		40: 4	
42		18: 1	0: 0		0: 0		30: 3	
43	33: 2		0: 0		25: 4		49: 3	
44		4: 0	0: 0			4: 1		3: 1
45	9: 1			0: 0		4: 1		4: 1
46		16: 1		0: 0		0: 0		20: 1
47		2: 1	5: 0			19: 1	33: 2	
48		0: 0		2: 0		1: 1	29: 3	

Bird: SC18
Food Tone: 1

Trial	Discrimination 3 Food K: R	Discrimination 3 Food K: R	Testing 1 Food K: R	Testing 1 None K: R	Testing 2 Food K: R	Testing 2 None K: R	Testing 3 Food K: R	Testing 3 None K: R
1	43: 7		0: 0		43: 6		71: 6	
2	2: 0		0: 0		70: 5			1: 1
3	0: 0			0: 0		3: 1		0: 0
4		59: 6		0: 0	29: 5		61: 7	
5	61: 7			0: 0	52: 6			3: 1
6	64: 6			0: 0		16: 1		6: 1
7		66: 4	0: 0		0: 0			4: 1
8	9: 0		0: 0		0: 0		46: 6	
9		34: 5	0: 0		44: 3		91: 5	
10	0: 0		0: 0			0: 0	66: 6	
11	0: 0		0: 0			0: 0	55: 6	
12		0: 0	0: 0		0: 0			1: 1
13		63: 6		0: 0		0: 0	68: 6	
14	12: 1		0: 0			2: 0		9: 1
15		2: 0		0: 0		1: 1		1: 1
16		0: 0	0: 0			0: 0		10: 0
17		25: 1		0: 0		0: 0		0: 0
18	0: 0			0: 0		0: 0		2: 0
19	24: 3		0: 0		0: 0			0: 0
20	0: 0		0: 0		0: 0		58: 6	
21	0: 0			0: 0	0: 0			0: 0
22	0: 0		0: 0		0: 0		0: 0	
23	0: 0		0: 0			0: 0	39: 3	
24		7: 0	0: 0		0: 0		72: 5	
25	0: 0			0: 0		0: 0		2: 1
26		0: 0		0: 0		0: 0	52: 4	
27		2: 0		0: 0		0: 0		12: 0
28		63: 6		0: 0		0: 0		8: 1
29	0: 0		0: 0		0: 0		10: 0	
30	54: 6			0: 0		0: 0		3: 0
31		0: 0		0: 0	0: 0		0: 0	
32		28: 2	0: 0			0: 0		0: 0
33		0: 0		0: 0	0: 0		2: 0	
34	2: 0			0: 0	0: 0			0: 0
35	0: 0			0: 0	0: 0		0: 0	
36		0: 0	0: 0		0: 0		0: 0	
37		0: 0	0: 0			0: 0		0: 0
38	45: 6			0: 0	0: 0			0: 0
39		60: 3	0: 0		0: 0		0: 0	
40		29: 2		0: 0		0: 0	0: 0	
41	49: 5			0: 0	0: 0		61: 5	
42		36: 2	0: 0		0: 0		46: 3	
43	0: 0		0: 0		0: 0		0: 0	
44		16: 1	0: 0			8: 0		0: 0
45	32: 2			0: 0		0: 0		0: 0
46		1: 0		0: 0		0: 0		1: 1
47		0: 0	0: 0			0: 0	42: 4	
48		18: 2		0: 0		0: 0	0: 0	

Bird: SC19
Food Tone: 2

Trial	Discrimination 3 Food K: R	Discrimination 3 Food K: R	Testing 1 Food K: R	Testing 1 None K: R	Testing 2 Food K: R	Testing 2 None K: R	Testing 3 Food K: R	Testing 3 None K: R
1	82: 8		66: 10		72: 8		103: 9	
2	79: 7		113: 7		85: 8			10: 1
3	84: 7		63: 5		53: 8		77: 9	
4	82: 8			5: 1	56: 7			19: 1
5	83: 6			2: 0	40: 3		88: 7	
6	6: 0			0: 0		2: 1		11: 1
7		0: 0	0: 0			0: 0		17: 1
8	59: 5		0: 0		0: 0		79: 6	
9	68: 5			0: 0		0: 0	80: 8	
10		0: 0	0: 0			19: 1	38: 7	
11	0: 0			0: 0		7: 1		15: 1
12	0: 0		0: 0			0: 0		20: 1
13		35: 3		0: 0		0: 0	30: 3	
14		48: 4	37: 4			0: 0		10: 1
15	6: 0			15: 1	0: 0			16: 1
16		56: 5		7: 1	86: 7		77: 7	
17	51: 3			13: 1		0: 0		13: 1
18		53: 6	75: 6		0: 0			2: 1
19	0: 0			1: 1		0: 0		6: 1
20	52: 6			5: 1	23: 2		92: 8	
21	46: 2		66: 7			1: 1		7: 0
22		95: 8	0: 0			18: 1		2: 0
23		38: 6		7: 1	93: 8		0: 0	
24		68: 6		14: 1	62: 5		5: 1	
25		69: 7	82: 7			2: 1	0: 0	
26	0: 0		0: 0			16: 1		0: 0
27	69: 7		64: 6		0: 0			0: 0
28		45: 4	52: 6			5: 1	0: 0	
29	79: 8		59: 8		29: 3		88: 8	
30		80: 8	41: 6		84: 7			13: 1
31		58: 7		1: 1	16: 3		83: 8	
32		29: 2		2: 1	74: 8			4: 1
33		84: 6		15: 1		14: 1	78: 8	
34		52: 7		5: 1	67: 6		74: 7	
35		49: 7	90: 6			12: 1		9: 1
36		65: 5	52: 7		95: 6		67: 8	
37		57: 4	36: 4		76: 7		63: 7	
38	65: 7		89: 8			15: 1		14: 1
39	83: 6			5: 1		9: 1	85: 8	
40	64: 6		74: 6		82: 9			0: 0
41		79: 8		6: 1	81: 7			1: 1
42	77: 6			13: 1	69: 8		95: 7	
43	71: 7			18: 1		4: 1		4: 1
44		52: 6	100: 8			17: 1	107: 6	
45	0: 0			20: 1		7: 1	87: 6	
46		54: 4	90: 7			15: 1	85: 8	
47		26: 3		14: 1		15: 1		3: 1
48		74: 6		9: 1	72: 8			10: 1

Bird: SC20
Food Tone: 2

Trial	Discrimination 3		Testing 1		Testing 2		Testing 3	
	Food K: R	Food K: R	Food K: R	None K: R	Food K: R	None K: R	Food K: R	None K: R
1	0: 0		68: 8		60: 9		67: 6	
2	69: 8		68: 8		62: 8			16: 1
3	88: 5		61: 8		64: 6		84: 7	
4	49: 5			14: 1	46: 3			16: 1
5	27: 1			0: 0	59: 6		83: 7	
6	39: 3			0: 0		9: 1		6: 1
7		31: 3	49: 6			18: 1		18: 1
8	25: 2		73: 6		60: 6		81: 6	
9	18: 2			15: 1		11: 1	71: 5	
10		68: 7	0: 0			4: 1	63: 6	
11	45: 3			0: 0		15: 1		2: 1
12	63: 5		0: 0			2: 1		15: 1
13		82: 7		20: 1		12: 1	91: 7	
14		80: 5	0: 0			18: 1		5: 1
15	74: 7			0: 0	81: 7			13: 1
16		68: 7		0: 0	68: 7		72: 8	
17	76: 6			0: 0		17: 1		4: 1
18		56: 6	0: 0		79: 7			4: 1
19	69: 6			13: 0		17: 1		13: 1
20	72: 8			5: 1	71: 6		80: 9	
21	55: 5		0: 0			5: 1		10: 1
22		52: 6	0: 0			4: 1		19: 1
23		67: 9		0: 0	75: 8		85: 7	
24		64: 6		15: 1	68: 6		66: 7	
25		84: 7	0: 0			2: 1	71: 8	
26	69: 7		0: 0			20: 1		15: 1
27	85: 5		0: 0		71: 6			4: 1
28		80: 8	7: 0			0: 0	86: 7	
29	73: 7		68: 7		0: 0		85: 7	
30		85: 7	73: 8		72: 4			2: 1
31		90: 9		19: 1	63: 6		96: 8	
32		92: 6		0: 0	55: 8			17: 1
33		69: 8		20: 1		16: 1	72: 9	
34		88: 7		0: 0	59: 7		49: 9	
35		74: 8	0: 0			12: 1		1: 1
36		71: 6	68: 5		74: 8		102: 6	
37		92: 7	72: 6		77: 7		78: 9	
38	78: 6		42: 6			18: 1		14: 1
39	57: 5			3: 1		15: 1	92: 7	
40	71: 5		15: 1		0: 0			7: 1
41		76: 6		16: 1	66: 5			20: 1
42	51: 6			0: 0	60: 9		73: 8	
43	81: 7			0: 0		4: 1		1: 1
44		65: 8	0: 0			11: 1	85: 8	
45	68: 6			0: 0		7: 1	78: 8	
46		52: 5	70: 6			6: 1	66: 9	
47		54: 5		3: 1		19: 1		5: 1
48		67: 7		0: 0	56: 8			19: 1

Appendix V: Published papers

The following three papers (re-prints of which follow) have been published by the author:

Rutter, S.M. and Duncan, I.J.H., 1988. Measuring fear in domestic fowl using aversion learning. In: J.Unshelm, G. van Putten, K.Zeeb and I.Ekesbo (Editors), *Proceedings of the International Congress on Applied Ethology in Farm Animals, Skara, Sweden.* KTBL, Darmstadt, pp.108-109.

Rutter, S.M. and Duncan, I.J.H., 1989. Behavioural measures of aversion in domestic fowl. In: J.M.Faure and A.D.Mills (Editors), *Proceedings of the Third European Symposium on Poultry Welfare, Tours, France.* WPSA, Tours, pp.277-279.

Rutter, S.M. and Duncan, I.J.H., 1989. Learning as a measure of aversion (Abstract). *Applied Animal Behaviour Science*, **24**: 84.

MEASURING FEAR IN DOMESTIC FOWL USING AVERSION LEARNING

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Abstract

Two techniques, namely shuttle avoidance and conditioned suppression were used to assess the aversiveness of states of fear to the fowl. One strain of laying hens generally learnt to perform a shuttle avoidance response during the presentation of a conditioned stimulus (light) paired with an aversive unconditioned stimulus (a rapidly inflating balloon), whereas a second strain generally failed to learn the response. Consequently, shuttle avoidance is not believed to be a robust enough phenomenon to act as a reliable measure.

Hens which failed to learn the avoidance response did subsequently show suppression in operant responding during the presentation of the conditioned stimulus. Conditioned suppression is therefore believed to be robust enough to be used as a measure of fear.

1 Introduction

In recent years there has been increasing public concern about the welfare of intensively reared domestic livestock, particularly battery-caged hens. It has been suggested that hens kept under such conditions will be frightened and frustrated (Command Paper 2836, 1965). However, both physiological and comparative behavioural measures of fear have been criticised as they only measure the animal's responses to aversive stimuli and not the motivational state behind them. Perhaps a more promising approach is to see if particular aspects of intensive systems will act as negative reinforcement in aversion learning (Dawkins 1980).

Aversion learning techniques were, however, developed by psychologists to study learning and not as measures of aversion per se. Therefore it is important that the techniques are validated as measures before being used to assess fear in commercially reared animals.

This paper reports an investigation into the validity of two of these techniques. Shuttle avoidance requires a bird to learn to perform a response during a conditioned stimulus in order to avoid an aversive unconditioned stimulus. Conditioned suppression measures the extent to which a conditioned stimulus paired with an aversive stimulus suppresses operant behaviour.

2 Experiment 1 - shuttle avoidance

2.1 Materials and Methods

The birds were tested in a two-compartment box (each compartment 0,90 m x 0,60 m x 0,60 m) known as a shuttle-box. A doorway (0,18 m x 0,45 m) between the two compartments allowed the bird free access to either side of the box. The conditioned stimulus (CS) was a panel lamp and the unconditioned stimulus (US) was a rapidly inflating balloon. Domestic hens find an inflating balloon very frightening, and it provides a potent, but controlled aversive stimulus. Each side of the box was fitted with a balloon and a light. Food and water were available ad libitum in both compartments.

For the experimental treatment, the light was switched on for 10 s before the balloon was inflated. However, if the bird moved into the other compartment during the presentation of the light (the avoidance response), the balloon was not inflated. As a control treatment, the light and balloon were presented at random i.e. there was no explicit association between the two. The birds were tested until they reached a criterion of learning of avoiding the balloon on five consecutive trials, or to a maximum of 30 trials. The inter-trial interval was randomly varied between 6 and 12 min. The birds were given 24 hours pre-exposure to the equipment prior to the testing session.

To test the generality of the procedure, two different strains of laying hen known to differ in their responses to fear (DUNCAN and FILSHIE 1979) were used. T-line birds were derived from Light Sussex and Rhode Island Red breeds and are usually described as docile. S-line birds were derived from the White Leghorn breed and are usually described as flighty. Ten birds of each strain received the experimental treatment and ten the control treatment.

2.2 Results

As the performance of birds which learnt the avoidance response was measured on a different scale to those which did not (i.e. number of trials to criterion compared with the proportion of avoidance trials) the data were not suitable for parametric analysis. Therefore, the Mann-Whitney non-parametric statistical test was used to analyse the results.

Of the forty birds tested, only eight reached the criterion of learning. Of these eight, seven were from the T-Line experimental group and one was from the S-Line experimental group.

Both the T-line and S-line experimental groups showed more avoidance behaviour than their respective controls ($U = 0$, $p < 0{,}002$; $U = 13{,}5$, $p < 0{,}01$), and the T-line experimental group showed more avoidance than the S-line experimental group ($U = 7$, $p < 0{,}01$). There was no significant difference between the T-line control and the S-line control groups ($U = 40$, $p > 0{,}1$), and there was no significant strain-treatment interaction ($U = 153{,}5$, $p > 0{,}1$).

2.3 Discussion

The T-line experimental group generally learnt to avoid the balloon. Although the S-line experimental group showed a significantly greater amount of avoidance behaviour than the S-line controls, the majority of the S-line birds failed to meet our criterion of learning. Why should this be the case?

In this experiment, a bird had to learn two distinct associations in order to avoid the aversive stimulus. First, it had to learn the association between the conditioned and unconditioned stimuli in order to predict the impending fright. It then had to learn that by moving into the other side of the box it could avoid being frightened. It is possible that either one or both of these stages was missing or impaired in the S-line birds.

The birds were, therefore, tested to see if they had learnt the association between the light and the balloon using conditioned suppression.

3 Experiment 2 - conditioned suppression

3.1 Materials and methods

The birds used in Experiment 1 were taught to perform an operant response to gain access to food whilst in the shuttle-box. The birds had to peck at a trans-illuminated plastic disc in order to open a door, which gave them access to food for 5 s. The birds were reinforced with the food on a variable interval 1 min (VI 1) schedule, i.e. the first response made after an interval, which was randomly varied between 1 and 119 s, was reinforced. The responses were recorded and the system controlled by a microcomputer.

The birds received four test sessions with the lights and balloons during which the experimental and control treatments were as in Experiment 1, except that the duration of the CS was increased to 1 min. These were followed by four extinction sessions, during which only the conditioned stimulus was presented. The birds were deprived of food for 24 hours before each session. Each session was composed of three trials and lasted one hour.

Due to a number of the birds dying during the interval between the two experiments, the number of subjects in each group was reduced from ten to five.

3.2 Results

The mean operant response rate for all of the birds within each group is shown in table 1. All the T-line experimental birds showed complete suppression of operant responding during the CS. The figure of 0,5 for the response rate of the S-line experimental group during the presentation of the CS was due to one bird which had habituated to the US; the other S-line experimental birds all showed total suppression i.e. response rate 0.0, during the CS. Although the control groups showed some suppression, this was not complete.

Table 1: Mean number of operant responses in the minute before and the minute during the presentation of the conditioned stimulus

strain	treatment	testing sessions 2 to 4		extinction sessions 6 to 8	
		before CS	during CS	before CS	during CS
T-line	experimental	7,2	0,0	10,7	3,2
S-line	experimental	3,7	0,5	9,5	1,9
T-line	control	3,9	0,8	11,7	8,3
S-line	control	6,2	4,9	11,3	8,9

All five of the T-line experimental birds, but only two S-line experimental birds showed avoidance on 50 % or more of the test trials. All the control birds showed avoidance behaviour on less than 50 % of the test trials.

3.3 Discussion

The complete suppression of operant responding during the CS shows that the S-line experimental birds had learnt the light-balloon association and that the failure to avoid was due to them failing to learn the actual response needed to avoid. It is believed that their strain-specific defence reactions are incompatible with the response needed for avoidance; the birds wanted to fly rather than walk away from a potentially dangerous situation. This is

similar to BOLLES' notion of species-specific defence reactions (BOLLES 1970).

The T-line control group also showed suppressed operant responding during the CS, and this phenomenon has been noted in rats (QUINSEY 1971). This is believed to be due to the birds forming a general association between the CS and the US, even though they are not explicitly paired. However, responding during extinction recovered at a much greater rate than in the experimental group, indicating that the control group did not find the CS as aversive as the experimental group. Indeed, the recovery of responding during extinction provides a sensitive measure which can be used to discriminate between different levels of fear.

4 Conclusions

The general failure of the S-line birds to learn the shuttle avoidance task indicates that shuttle avoidance is not a suitable technique for measuring aversion.

The fact that all the experimental birds showed suppressed operant responding during the presentation of the conditioned stimulus indicates that conditioned suppression is a robust enough phenomenon to be used as measure of aversion. However, to allow discrimination between different levels of aversion, it is important to study the recovery of responding during extinction.

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BEHAVIOURAL MEASURES OF AVERSION IN DOMESTIC FOWL

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INTRODUCTION

Applied ethologists are increasingly using aversion learning techniques to assess the suffering caused by modern husbandry procedures. However, it is important that these techniques are validated before being used to measure the aversiveness of commercial practices (Rushen, 1986).

This paper reports an investigation into the validity of four of these techniques when used to assess aversion in domestic fowl.

MATERIALS AND METHODS

Two strains of laying hen were used; T-line, a medium bodyweight Rhode Island Red x Light Sussex hybrid, and S-line, a light bodyweight White Leghorn hybrid.

Experiments 1 and 2 involved a rapidly inflating balloon as the aversive stimulus, an indicator lamp as the warning stimulus, and a truly random control procedure i.e. the control group received both the warning and aversive stimuli but presented at random with no explicit association between the two.

Experiments 3 and 4 involved cage dusting with a feather duster as the

aversive stimulus, an auditory warning stimulus, and the control group received only the warning stimulus and not the aversive stimulus.

EXPERIMENT 1 : Shuttle Avoidance

The birds were tested in a shuttle box (Fig. 1). For the experimental treatment, the light was switched on for ten seconds before the balloon was inflated. The intervals between trials were randomly varied between six and twelve minutes. A bird was said to have avoided if it moved into the other compartment during the warning signal. A bird could therefore avoid being frightened by shuttling to and fro between the two compartments. The birds were tested either until they showed avoidance on five consecutive trials or to a maximum of 30 trials.

EXPERIMENT 2 : Conditioned Suppression

The food hoppers in each side of the shuttle box were replaced with operant panels and the birds from Experiment 1 were taught to peck at a switch in order to get a food reward. They were then tested as in Experiment 1 except the duration of the warning stimulus was increased to one minute. The operant response rates in the minute before and the minute during the warning signal were recorded.

EXPERIMENT 3 : One-way Avoidance

Birds were tested in a one-way box (Fig. 2). Sliding doors separated each of the compartments which could be illuminated separately. For the experimental treatment, the door to the next compartment was opened, the light source was switched to the next compartment and a buzzer was sounded. If after 10 seconds the bird had not moved into the next compartment it received a fright. The birds could therefore avoid being frightened by moving to the next compartment when the warning signal came on. All birds were tested for a total of 48 trials.

EXPERIMENT 4 : Passive Avoidance

A battery cage was fitted with an operant panel. Birds were first taught to perform the operant response. The operant panels were then programmed to give food reinforcement only during two tones. The tones were presented at random for two minute intervals separated by periods of silence which varied in duration from two to twelve minutes. The birds were given five days to learn this discriminative operant task. They then received three days of testing, in which operant responses performed during one of the tones continued to give food reinforcement, whilst responses during the other resulted in exposure to the aversive stimulus.

The birds could therefore avoid being frightened by ceasing operant responding during the 'fright' tone whilst still being able to feed by responding during the 'food' tone.

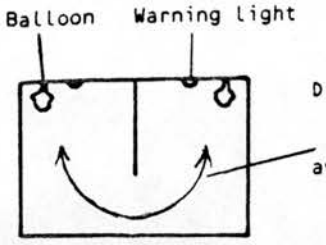

Figure 1. Shuttle box.

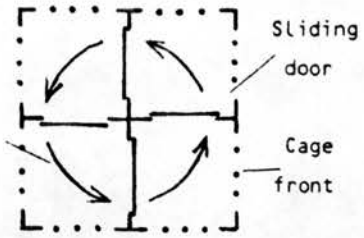

Figure 2. One-way box.

RESULTS AND DISCUSSION

Although the T-line birds generally learnt the shuttle avoidance task, only one out of the ten S-line birds reached the criterion of learning of five consecutive avoidance trials. Consequently, shuttle avoidance cannot be recommended. The S-line birds which failed the shuttle avoidance task did, however, show suppression of operant responding during the presentation of the warning stimulus, indicating that they had learnt the association between the light and the fright. Conditioned suppression can, therefore be recommended.

Both T-line and S-line birds generally learnt the one-way avoidance task. However, some T-line control birds also showed a significant amount of 'avoidance' behaviour, suggesting that the behaviour shown by birds receiving the experimental treatment may not have been true avoidance. One-way avoidance cannot, therefore, be recommended.

The passive avoidance task was, however, learnt quickly by the majority of birds tested, sometimes after as few as four exposures to the aversive stimulus. The control birds continued to respond during both tones i.e. showed no avoidance behaviour. Passive avoidance can, therefore, be strongly recommended.

REFERENCE

Rushen, J., (1986). The validity of behavioural measures of aversion: a review. Applied Animal Behaviour Science, 16: 309-323.

SUMMARY

Four aversion learning techniques are described. Shuttle avoidance and one-way avoidance were not found to be very robust and cannot, therefore, be recommended for use in welfare assessment. Passive avoidance, however, was generally learnt quickly by the majority of subjects tested. Consequently, its use is strongly recommended.

Learning as a Measure of Aversion

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ABSTRACT

Aversion learning techniques developed by psychologists are being used increasingly by applied ethologists to measure aversion in domestic animals in an attempt to measure the suffering caused by modern husbandry procedures. However, before using these techniques to measure the aversiveness of commercial practices, it is important to assess their validity. Rushen (1986) proposed that their empirical validity (i.e., the ability to discriminate between known degrees of aversion) could be tested by studying the effects of the intensity or duration of electric shock. However, electric shock is a very unnatural stimulus, and the exact relationship between shock severity and aversion is not yet clear.

An alternative approach to selecting the most appropriate aversion learning technique for welfare assessment is therefore proposed. Firstly given the wide range of fear levels shown by different individuals to the same stimulus, it is important that any consideration of welfare is based on data from as many individuals as possible. The task should, therefore, be learnt by the majority, if not all, of the animals tested. Secondly, the task should be learnt after a minimum number of exposures to the aversive stimulus in order to ensure that habituation does not confound the experimental design. Thirdly, the chosen technique should then be tested with a variety of treatments believed to differ in their aversive properties. The technique can then be validated by comparing the recorded levels of aversion with the various treatments with other behavioural and physiological indices of suffering (e.g. heart rate).

REFERENCE

Rushen, J., 1986. The validity of behavioural measures of aversion: a review. Appl. Anim. Behav. Sci., 16: 309-323.